

NOTES ON
WOODPECKERS (PICIDAE)



BY
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NOTES ON WOODPECKERS (PICIDAE)

By D. GOODWIN

THESE notes are based on examination of the woodpeckers, Picidae, in the British Museum (Natural History) during revision and re-arrangement of the collection. The only species I know in life are the Green Woodpecker *Picus viridis*, the Greater Spotted Woodpecker *Dendrocopos major* and the Lesser Spotted Woodpecker *D. minor*; I have also briefly observed the Grey-headed Woodpecker *Picus canus*, the Black Woodpecker *Dryocopus martius*, the Syrian Woodpecker *Dendrocopos syriacus*, the Middle Spotted Woodpecker *D. medius*, the Hairy Woodpecker *D. villosus*, the Downy Woodpecker *D. pubescens*, the Sapsucker *Sphyrapicus varius*, the Red-bellied Woodpecker *Melanerpes carolinus* and the Golden-shafted Flicker *Colaptes auratus* during visits to Austria and North America.

Suggestions or conclusions presented here are, therefore, based mainly on external morphological characters. For this reason I have not suggested alterations from the most recent comprehensive check list (Peters, 1948) except when the evidence in favour of such a course appears overwhelming.

Section I: General notes on the family

REMARKS ON AFFINITIES, CONVERGENCE AND COLORATION

Peters (1948) divides the true woodpeckers (Picinae) into two major groups on the basis of correlated foot and bill characters: those in which the outer hind toe is not longer than the outer front toe, the nasal shelf narrower and the nostril near the culmen; and those which have the outer hind toe longer than the outer front toe, a wider nasal shelf, and the nostril mid-way between the culmen and the edge of the upper mandible or nearer the latter. When the woodpeckers are thus divided into two groups two significant correlations emerge. First, most, if not all, genera, many or all of whose members are known to be partly or entirely ground feeders, or to feed largely by picking insects from the surface of trunks, branches or leaves or by fly-catching, come into the first group. This is the case with *Nesocoleus*, *Picus*, *Dryocopus*, *Melanerpes*, *Asyndesmus*, and *Micropternus*. Second, some "pairs" of genera whose geographical distributions, colour patterns and general similarity suggest close relationships between them—*Geocolaptes* and *Mesopicos*, *Micropternus* and *Blythipicus*, and *Dinopium* and *Chrysocolaptes*—are separated. Thus it seems likely that these bill and foot differences may be rather labile adaptive characters and that the toe formation may have become differentiated in closely related forms in the course of adaptive radiation.

In Europe woodpeckers divide easily into four taxonomically distinct genera—*Picus*, *Dryocopus*, *Dendrocopus* and *Picoïdes*—with no troublesome intermediate forms. The same does not hold true for most other geographical regions. Even such visually striking differences in coloration as those between "pied" woodpeckers and "green" woodpeckers are bridged by "pied" woodpeckers that show considerable yellow or green suffusion, such as *Dendrocopos temminckii* and *Melanerpes*

striatus; and by "green woodpeckers, such as *Veniliornis spilogaster*, which, show an underlying pattern virtually identical to that of some of the black and white forms. As in other groups of birds there is evidence that relatively concolorous forms with a simplified colour pattern can derive from forms with a more complex pattern, although in the woodpeckers most of these are still at a stage where their affinities are obvious; for example *Melanerpes herminieri* and *Sapheopipo noguchii*.

The following general trends in coloration and colour pattern are evident. Forest forms tend to have boldly patterned black and white colour patterns, usually with red or yellow signal or display markings. Forms inhabiting more open woodland are usually more cryptic; either through a predominantly olive-green colour, at least on the upper parts; or, when predominantly black and white in coloration, through a barred ("ladder-backed") or profusely mottled pattern. Forms that have become largely terrestrial tend to be more fully cryptically coloured, and show reduction or absence of the red or yellow markings on crown or nape that are otherwise so nearly universal in the woodpeckers. In view of the number of species whose behaviour and ecology are little known the above remarks are, of course, tentative. On the other hand, apparent exceptions to those general rules may prove not to be so when we have further information. For example, the Syrian Woodpecker *D. syriacus* which is black and white with a red nuchal patch in the male inhabits, at least in its European range, rather open cultivated and settled regions, but this choice of open habitat may be, in an evolutionary sense, a recent development. Again, the Green Woodpecker *P. viridis* feeds largely on the ground through it appears colourful enough at close quarters. When, however, it is on the ground in typical feeding sites, such as grassy slopes, parkland, and woodland openings, its plumage is highly procryptic and even the red on its head, which is darker and less "fiery" in tone than that of many more arboreal species, does not show up very conspicuously. It must be mentioned that conspicuous red, yellow or white rumps can be concealed by the folded wings, and they usually are when their owners are alarmed, so that their possession by such species as the Ground Woodpecker *Geocolaptes olivaceus* and the Andean Flicker *Colaptes rupicola*, does not significantly affect the cryptic character of the rest of their plumage.

There are widely separated allopatric forms that show considerable general resemblance to each other. In some cases the details of their respective colour patterns make it fairly certain that the resemblance is due to convergence. This is so, for example, with the two ground-living woodpeckers, *Colaptes rupicola* of South America and *Geocolaptes olivaceus* of South Africa, whose affinities are clearly with other American and African forms respectively, not with each other. The Chestnut-coloured Woodpecker *Celeus castaneus* of Central America is related most closely to other *Celeus* species, and thence to other American genera, and is, obviously, not at all closely allied to the Asiatic Rufous Woodpecker *Micropternus brachyurus*, to which its rufous, black-barred plumage gives it considerable superficial resemblance. The small green woodpeckers of Central and South America, of the genus *Veniliornis*, show such close resemblance to the African genera *Dendropicos* and *Campethera* that I feel uncertain whether this is due to genuine close affinity or to convergence, although I think the former less likely.

The Ethiopian region has no arboreal woodpecker that is very large in size. Although the smallest woodpeckers in the Nearctic, Neotropical and Oriental regions are all about the same size, the largest arboreal African woodpeckers (*Thripias*) are much smaller than the largest arboreal species in all the other woodpecker-inhabited regions. The largest African species, the terrestrial *Geocolaptes olivaceus*, is, however, about the same size as, or only a little smaller than species that are equally (*Colaptes rupicola*) or to some considerable extent (other *Colaptes* species, some *Picus* species) terrestrial in the Nearctic, Palearctic and Neotropical regions. Also no African woodpecker is boldly black and white in colour although the African barbets have produced some predominantly black and white species.

Another interesting fact is that although all other continents inhabited by woodpeckers have several very similarly coloured "green" woodpeckers, there are no green species in North America, where their ecological equivalents would seem to be the brownish and barred flickers, *Colaptes*, and the "ladder-backed" species of *Melanerpes* (*Centurus*).

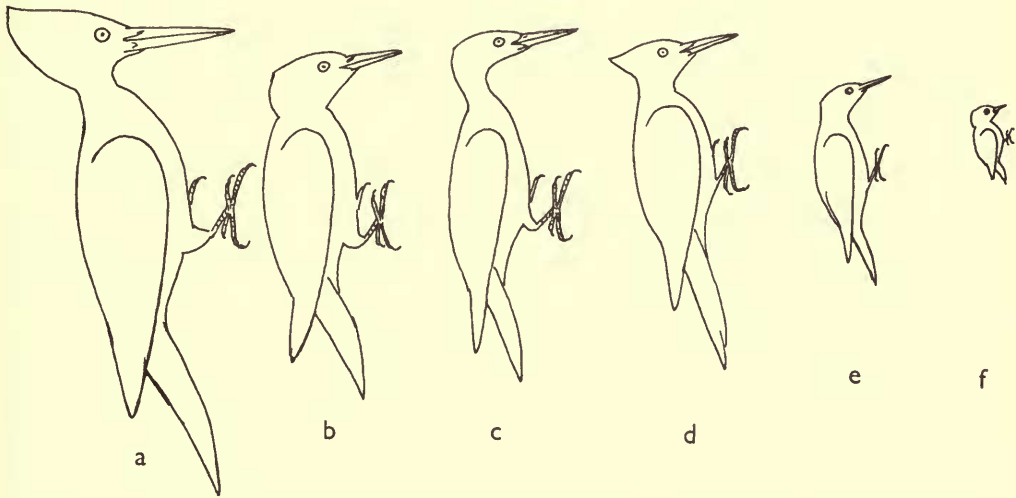


FIG. 1. (a to e) Diagrammatic outline sketches of the largest species of arboreal woodpecker in, respectively, the Nearctic, Palearctic, Oriental, Neotropical and Ethiopian regions; f shows comparative size of the smallest woodpecker species (piculets excluded) in all of the above regions. It should be noted that the largest Nearctic species, the Imperial Woodpecker *Campephilus imperialis*, is rare and restricted in range; the largest widespread species in the Nearctic, the Pileated Woodpecker, *Phloeocaeates pileatus*, is approximately the same size as the largest species in each other region, the Ethiopian excepted.

SEXUAL DIMORPHISM

The great majority of woodpeckers are sexually dichromatic. In nearly all the difference consists of the male having red or, less often, yellow areas on the head that are absent in the female. This may involve only the male having red on the head or both sexes may have heads that are predominantly red in colour but still with the

female having a little less than the male. Even in species such as *Colaptes rupicola* and *Micropternus brachyurus*, in which the male has only a little rather dull red on the malar region, the sexual distinction is clear cut and not just a matter of the male being slightly brighter or having his bright colours slightly more extensive than the female's. This latter form of sexual dichromatism, common in so many birds, is found in only a very few woodpeckers.

Only in five species are the sexes alike or nearly so. These are the Middle-spotted Woodpecker *Dendrocopos medius*, the Sapsucker *Sphyrapicus varius* (the predominantly red-headed races *daggetti* and *nuchalis*) Lewis's Woodpecker *Asyndesmus lewis*, the Red-headed Woodpecker, *Melanerpes erythrocephalus* and the Porto Rican Woodpecker *M. portoricensis*. In *D. medius*, both sexes have the crown red, a very common feature of males of allied *Dendrocopos* species. There is, however, some sexual difference in that the red on the female is not quite so bright as on the male and does not usually reach quite so far back on the nape where it is tinged with yellow. This is the kind of sexual dimorphism common to most bird species in which the sexes are usually said to be alike. It would, presumably, not give so immediate or positive a clue to sex as the type of difference usual in woodpeckers. In the red-headed form of *S. varius* there is also a marginal tendency for the male to be more intensely coloured, but in *M. erythrocephalus* there is no constant difference in brilliance between the sexes. There does not seem any obvious or likely reason why any of these three forms should be able to dispense with the usual type of sexual dimorphism which, since it is nearly universal, must have, in most species, strong selective value. *D. medius* is, however, sympatric with congeneric and rather similar species, and in its case selection for specific distinctness may have operated at the expense of sexual differentiation. One species that is in many places sympatric with it, *D. leucotos*, is extremely similar in coloration and colour pattern except that the female has a black instead of a red crown; it is also larger in size.

Asyndesmus lewis is a rather aberrant species which differs much in feeding habits from the more typical woodpeckers (see Bent, 1939). Its colour pattern, although showing some connections with those of some *Melanerpes* species, to which it is clearly allied, is unusual and it has no red on crown or nape. Typically the female is marginally duller than the male. *M. portoricensis* shows in extreme degree the loss of distinctive markings common in isolated island forms, being all black except for a dark reddish tinge on the underparts. The sexes are alike.

Colaptes auratus is the only species which shows both conspicuous red markings (a red nuchal band) and clear cut sexual dimorphism that does not involve a lack of red in the female, the male alone having black malar stripes. Other flickers, leaving aside for the moment the aberrant Fernandina's Flicker *Nesocoeleus*, differ sexually in the male having red or partially red malar stripes and the female not. In *C. pitius* the red on the malar stripes of the male is reduced to a pale, dull pink on the tips of the feathers, whose bases are blackish, so that the sexual difference in this species is somewhat intermediate in character between that of *auratus* and other flickers although less conspicuous than in either.

The only woodpeckers in which neither sex shows a trace of red or yellow in the plumage are *Nesocoeleus fernandinus* and the Heart-spotted Woodpecker *Hemicircus*

canente. In *Nesoceleus* the sexes differ in the male having a black and the female a speckled malar stripe; in *H. canente* the male has the forehead and crown white, the female has a spotted forehead and crown.

Besides the colour differences described above female woodpeckers, like the females of most other birds, often average slightly smaller in bill size than the males. In some island forms this difference and the correlated difference in body size is considerable. In a recent important paper on this subject (Selander, 1966) it has been shown that such differences are correlated with sexual differences in feeding ecology and serve to lessen or prevent feeding competition between male and female.

The piculets, sub-family Picumninae, show "typical" woodpecker sexual dimorphism except that in two species the "male's" colour is chestnut, not pure red or yellow.

JUVENILE PLUMAGES

Juvenile woodpeckers, like juvenile barbets, Capitonidae, but unlike most other birds, usually show similar bright red or yellow pigments to those of the adults. In some species, of which the Greater Spotted Woodpecker *Dendrocopos major* is an example, the juvenile male may have differently placed and more extensive red markings than his father, and the juvenile female show red areas that are lacking in the adult female.

Many juvenile woodpeckers have a greater number of attenuated tail feathers similar in character to the stiff, central feathers used to prop the bird when resting or working on a tree trunk than have the adults. The juvenile's wing may show a reduction in size of the two innermost primaries and consequently rather more pointed wing. These facts prompted Kipp (1956) to suggest that the juvenile plumages of woodpeckers represented a probable future stage in their evolution as they could, he thought, neither represent a recapitulation of a prior evolutionary stage nor be of value to the juvenile as distinct from the adult. Verheyen (1957) disagreed with this conclusion; pointing out that, in many other birds, the juvenile rectrices are to some degree narrower and more pointed than the adult's and that the reduction in size of the inner primaries was probably connected with the need for quick growth to enable the early onset of the first moult. This was also discussed by Sibley (1957), who pointed out that this reduction of the innermost primaries occurs in some species only, and is almost certainly adaptive. The Stresemanns (1966) in their comprehensive study on moult in birds agree with this conclusion.

Verheyen also emphasized, correctly, that the juvenile plumage of woodpeckers is, like that of most other birds, usually of a weaker and more downy character than the adult plumage. He suggests that this might be of particular disadvantage to a woodpecker and hence one reason for the quick onset of the first moult. This, in some species, begins before fledging, at which time the two reduced inner primaries above mentioned, may have been replaced by adult feathers. Verheyen suggested that the bright red or yellow pigments of juvenile woodpeckers, and the fact that in many woodpeckers the juveniles show the same sexual dimorphism as the adults, might be due to an original (presumably duller and less dimorphic) juvenile plumage

having been completely suppressed in the course of evolution. He considered that the present juvenile plumage was originally the first post-juvinal dress. I think this is an unlikely hypothesis. Except for the bright red or yellow pigments often present, this plumage has the typical characteristics commonly found in juvenile plumages in other groups: a looser and more downy or woolly texture of the contour feathers; weaker shafts of the quill feathers; a tendency for transverse barring, dark or light shaft streaks or pale feather tips (not present or not so pronounced in adult) to be present or more prominent and to give a more spotted or barred general appearance and a tendency for black areas to be browner and less glossy. *All* these characters are not, of course, usually found in the juvenile plumage of any one species.

The red or yellow pigments themselves may be less fully developed in the juvenile plumage. The red is often lighter or more orange-red than that of the adult; and in many species the red tips of the feathers are less extensive, so that the juvenile appears to have a scattering of red speckles where the adult, if in unworn plumage, appears uniform red. In a few cases the lighter red of the juvenile may make it appear more brilliant. Similarly, in those species which have golden yellow instead of red on the head, this is often of a darker and more orange tint in the juvenile. It is possible, however, that in both these instances the juveniles may not appear more impressive to avian as they do to human eyes.

Verheyen divided the African and Eurasian species he studied into four groups: those in which the juveniles resembled the respective adults in their degree of sexual dimorphism; those in which the juveniles resembled neither parent; those in which both sexes resembled the adult male, and those in which both sexes resembled the adult female. Most other woodpeckers fall into one or other of Verheyen's categories, which do not, however, cover the whole range of juvenile plumages. It seems worthwhile to describe briefly the likenesses and differences (*vis à vis* the adult) found in the coloration and sexual dimorphism of the juvenile plumages, and their generic distribution. In so-doing I shall not take account of such minor differences as are generally characteristic of juvenile plumage. Thus a juvenile may be said to be "like the adult" if it has the same colour pattern and general coloration, even though it may, for example, have an orange-red instead of a scarlet cap.

It seems pertinent to digress here to mention the hazards when ascertaining the juvenile plumage in species of which few reliably sexed juvenile specimens are available. It has become very evident in the course of this study, that in the past many collectors have labelled young woodpeckers as males or females according to whether their head coloration most resembled that of the male or female adult. With well-known European and American species this guess-sexing is immediately obvious, but is much less easy to detect with species represented only by one or two specimens. Another hazard is that in some species, of which the Three-toed Woodpecker, *Picoïdes tridactylus* is an example, the feathers of the forehead and forecrown (sexually differentiated in the adult) are moulted very soon indeed after fledging, so that specimens in almost complete juvenile plumage, but with adult plumage on front and top of the head, may be much commoner in collections than birds in complete juvenile plumage.

In general colour pattern and the (usually sexually dimorphic) head markings,

juvenile plumages, come into one or more of the following categories. Categories 2 to 6 involve coloration of male juveniles, 7 to 9 of females, and 10 to 12 of both sexes.

(1) *The juvenile male and female are like respective adults in the extent of red or yellow on the head.*

In this category are some species of *Colaptes*, some (possibly all) species of *Piculus* and *Chrysoptilus*, some species of *Melanerpes* (*cruentatus*, *formicivorus*, *candidus* and possibly some others), *Trichopicus* (although in this species the yellow on the throat, which is not a sexual character, is absent in the juvenile), *Celeus flavescens* (most probably other species of *Celeus* also), some species of *Phloeocastus* (*lineatus*, *pileatus* and, probably, *schulzi* and *galeatus*), *Dryocopus*, *Picus* (with two possible exceptions and a tendency for restriction of lipochrome pigment in the juveniles of the yellow-naped species), *Gecinulus* (females of both species and males of one), *Dinopium benghalense* and *D. javanense* (but in the latter the front of juvenile's forehead is brownish so that it is intermediate in this character between *benghalense* and the other *Dinopium* species), *Chrysocolaptes* (*festivus* only; although the male of *validus* is very similar to the adult but has yellowish brown throat and malar region), *Dendrocopos* (males of all the red-crowned species and females of a very few species), *Meiglyptes* (but juvenile males often show a reddish tinge on forehead, which is rarer in adult males), *Blythipicus* (*pyrrhotis*), *Micropternus* (but a few juveniles show a trace of red on the nape).

(2) *The juvenile male has less extensive red or yellow areas on head than has the adult male.*

This broad category is best subdivided into the following groups.

(a) *Juvenile male has red (or yellow) only on the hind crown and/or nuchal region, adult male has entire top of head, and sometimes forehead also, red or yellow.* In this group belong the *Campethera* species. In *nubica*, *punctuligera* and *bennettii* juveniles resemble the adult female in having red only on the hind crown and nape, the forehead and forecrown is, however, more or less dull grey or blackish, not spotted or streaked with white as in adult female. In *maculosa* and *permista* the differences between adult and juvenile males are similar. Our few specimens of juvenile females of these species show less extensive red on the nuchal region than males. In *caroli* and *nivosa*, in which the adult females has no red and the adult male has red only on the nuchal region, the juvenile males appear to have no red and thus resemble the female. This statement is, however, based on only one juvenile male specimen of each species in our collection (which I have reason to believe were reliably sexed) and on Verheyen's description of *caroli*. In *Dinopium rafflesii* the juvenile male has the forehead brownish, shading to blackish on the crown with a few red flecks, narrow greenish gold fringes to some of the feathers and only the hind crown and long nuchal crest red; in *D. shorii* the juvenile male has the forehead streaked dark brown and dull cream; in both these species the adult males have the top of the head entirely red.

In *Chrysocolaptes lucidus* (*guttacristatus* and allied mainland races) the young male also lacks red on the forehead. This species shows, however, an interesting situation. The juvenile male at first has a brownish black forehead, unspotted or with only obscure spots. Before the juvenile plumage as a whole is shed some of the

forehead feathers are replaced by boldly spotted ones similar to those on the head of the adult female. These spotted feathers may extend well onto the crown where they have, presumably, replaced juvenile red feathers. Later these spotted feathers are replaced by red ones but some birds show feathers intermediate between the adult red feathers and the black and white spotted feathers, that is red feathers somewhat intermediate in form and with a white spot. These spotted feathers on the forehead do not seem to represent an intermediate plumage in any true sense but they do give the owner's head some "female" characteristics. From the available specimens it is difficult to judge whether differences are due to age or individual variation and observations on living birds are needed.

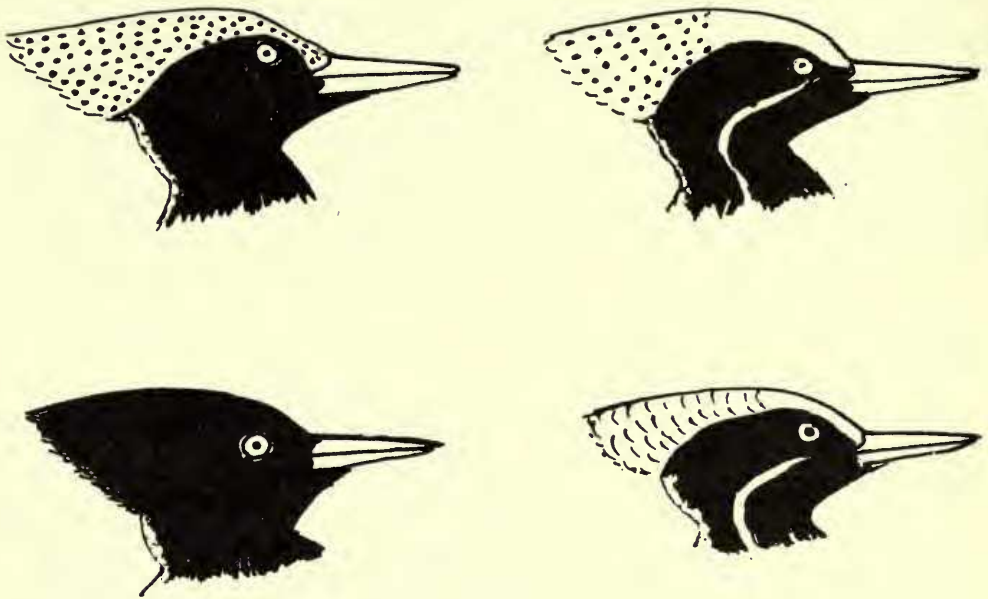


FIG. 2. Diagrammatic sketches of heads of *Hemicircus concretus* to show differences in colour pattern between adults (left) and juveniles (right) of both sexes; males above, females below. Shaded areas are dark grey, stippled areas bright red or orange-red, unshaded areas buff; the scale-like markings on the crest of the juvenile female represent grey feather edges.

Hemicircus concretus shows a striking difference between the juvenile and adult male. The latter has the entire top of the head, from forehead to nuchal crest, bright red, the rest of its head is dark grey. The juvenile male has the forehead and crown buff and only the nuchal crest (ends of the long head feathers) red. In the race *sordidus* the adult has the nuchal area largely grey and the juvenile male has much less red than in the juvenile of the nominate form. In both the juvenile shows a suggestion of a buff malar stripe which is lacking in the adult. It may be mentioned here that although the adult female's head and crest are grey the juvenile female is like the juvenile male except that her nuchal region is buff like her crown, not red.

(b) *Red on juvenile male does not extend to, or so far down, nape as in adult male.* In this group belong only the species of *Mesopicos*.

(c) *Adult male has head largely or entirely red; juvenile male has less red on head.*

Phloeocastes: in *guatemalensis* and *melanoleucos*, juveniles are like the adult female, thus having black forehead and forecrown and much less extensive red areas than adult males. In *robustus* (but this is surmised from only one specimen) the juveniles also, probably, resemble the adult female. In *haematogaster*, however, in which, as in *robustus*, the adult female has the forecrown red, the juveniles of both sexes have the forehead and forecrown blackish. They also have buff instead of red rumps although both on rump and head the juvenile feathers are soon replaced. In *leucopogon* the juveniles of both sexes are said (Laubmann, 1930) to have entirely black heads but this statement was based on one moulting juvenile. In *pollens*, the only form in which the female has no red on the head, an unsexed fledgling is like the adult female.

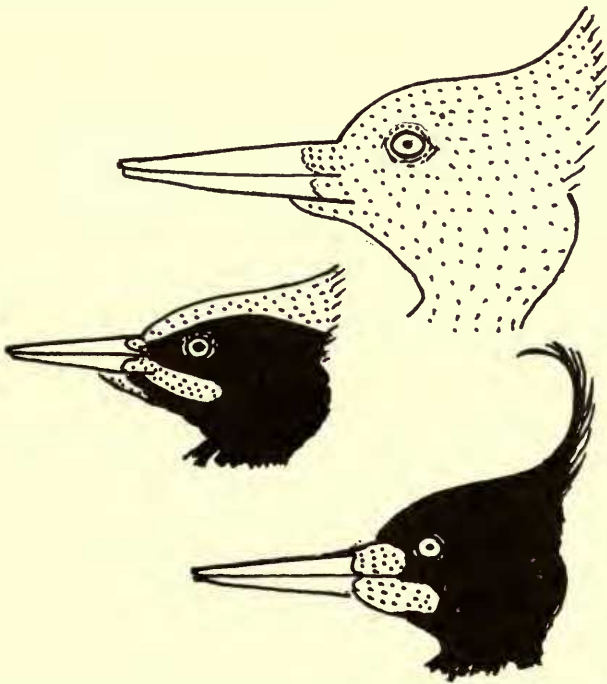


FIG. 3. Diagrammatic sketches to show difference in colour patterns of heads of adults (right) and juvenile male (left centre) of *Ipocrantor magellanicus*; the distribution of red and black on juvenile female is similar to adult female's.

In *Ipocrantor (magellanicus)* the male has the head entirely red; the juvenile male has a black head with forehead, crown, nape, malar stripes and chin red. Both juvenile and adult females have only the chin and loreal region red.

In the red-headed forms of *Sphyrapicus varius (ruber and daggetti)* the generally smoky-brown juvenile has the head extensively tinged with red but this red is not so extensive and not nearly so bright as that of the adult. So far as adult-juvenile

differences are concerned the situation is the same with those races of *varius* in which the adults have less red on the head.

(d) *Adult male has some red on head, juvenile male has none.*

In *Campethera nivosa* and *C. caroli* the adult males (but not the females) have red on the nape, although in *carola* this is reduced to a scattering of red-tipped feathers. If a male and a female juvenile of *carola* and a male juvenile of *nivosa* are correctly sexed, as I believe to be the case, then in neither of these species has the juvenile male any red on the head. The juvenile of *caroli* (both sexes) also differs in having less yellow pigment, in the top of its head being blackish brown instead of dark green and the yellow, dark-speckled throat and eye-stripe of the adult being replaced by pale brownish.

In the nominate form of *Sphyrapicus varius* the adult male has red crown and throat, the mainly brownish (instead of black and white) juvenile male has no red but it usually moults some or all of the feathers on its forehead and crown before it attains other parts of the adult dress. The juvenile male of *S. thyroideus* has the same black and white colour pattern as the adult male but has a white instead of a red throat.

There appears to be only one published description of a juvenile male of *Campephilus principalis* (Tanner, in Bent, 1939). This bird resembled in colour the adult female and lacked the red nuchal crest of the male (which extends forwards on sides of head). It did not begin to show red feathers until it was about 3½ months old. It is highly likely this is the normal situation and possible that some of the few other juveniles seen or collected, and sexed as females were, in fact, males also. It is also probable that the closely similar and possibly conspecific *C. imperialis* agrees with *principalis* in this.

(3) *Juvenile male has red (or yellow) on forehead and/or crown, adult male has this colour only on nuchal region.*

In this category are many species of *Dendrocopos*, one species (*rubiginosus*) of *Blythipicus* and, but to a marginal degree only, *Dendropicus fuscescens*. In this latter the red on the adult male's nape extends forward nearly to the crown.

(4) *Juvenile male has red on crown extending a little further towards forehead than red of adult male.*

In this category come all species of *Mesopicos* (3), both species of *Gecinulus* and, marginally, *Colaptes auratus* in which the juvenile male has a strong tinge of red on the crown.

(5) *Juvenile male and adult male both have red (or yellow) crown, this colour sometimes extending further over the nuchal region in the adult.*

This includes those species (many) of *Dendrocopos* in which the adult male has a red crown; *Mesopicos* (these come into category 4 also), *Thripas*, *Picoïdes*, *Dryocopus*, *Chrysocolaptes*; most species of *Dinopium* and *Picus*; some species of *Dendropicos* and some (possibly all?) species of *Veniliornis*.

(6) *Adult male has red only on malar region; juvenile male has red on forehead and crown also.*

Mulleripicus pulverulentus. I think it highly likely that the case is the same in *M. fuliginosus*, of which I have been unable to find either juveniles or descriptions

of them. *Meiglyptes* may show a suggestion of this condition, some male juveniles being tinged with red on the forehead.

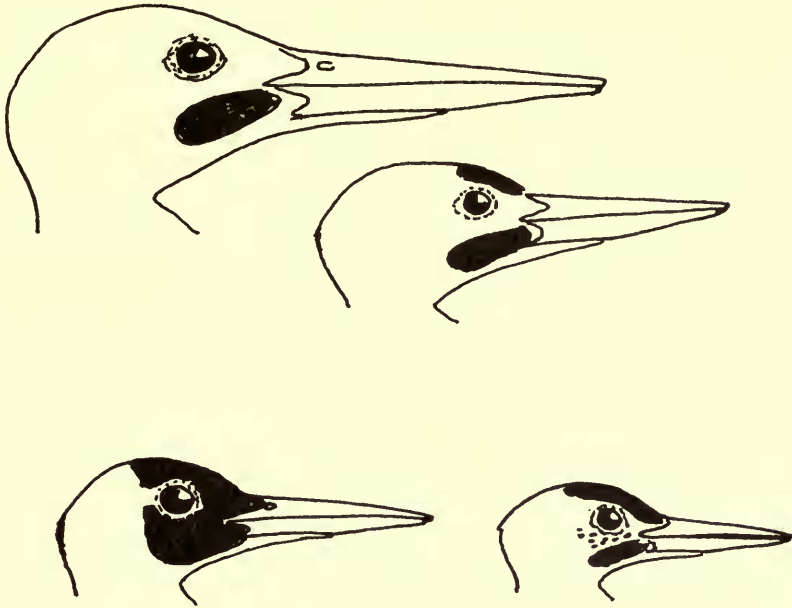


FIG. 4. Diagrammatic sketches to show colour patterns of heads of adult males (left) and juvenile males (right) of *Mulleripicus pulverulentus* and *M. fulvus*.

(7) Juvenile female resembles adult female in having no red on head, in species in which males have red on head.

Those species of *Colaptes* in which the males have red malar stripes; a few species of *Dendrocopos*, including the aberrant *D. albolarvatus*; some species of *Picus* (*squamatus* and its allies), *Meiglyptes*, *Chrysocolaptes* and *Dinopium* and in two related and rather aberrant species of *Campethera* (*nivosa* and *caroli*).

(8) Juvenile female and adult female differ appreciably in colour of head but neither has any red although the male has.

One species only, *Hemicircus concretus*, in which the adult female has the head (and most of the body) a concolorous olivaceous grey but the juvenile has the top of head and crest buff.

(9) Juvenile female has some red (or yellow) on head; none present in adult female.

Most species of *Dendrocopos*, *Picoïdes*, *Mesopicos*, *Thripias*, most species of *Dendropicos*, *Veniliornis callonotus* and, in all probability, other species of *Veniliornis* also.

(10) Juveniles of both sexes have strikingly different coloration and colour pattern from adults.

Melanerpes erythrocephalus. The juvenile appears predominantly greyish brown except on wings and tail owing to extensive pale brownish to brownish white fringes, central streaks and/or cross bars on the blackish cover feathers. There is only a little red around the eye, in contrast to the entirely red head of both sexes of the adult. The juveniles of the nominate form of *Sphyrapicus varius* (and to a lesser extent those of other forms of the species) are very similar in general coloration (and in the plumage patterns by which this is achieved) to the juvenile of *M. erythrocephalus* described above.

Hemicircus concretus comes less definitely into this category. The colour pattern of the juveniles (but not their coloration) is very close to the adult male's (see Text-fig. 2) but they also show some indication of a buff malar stripe which is lacking in the adults.

(11) *Adults differ in coloration and colour pattern, juveniles very like respective adults but juvenile male lacks the red throat of the adult male.*

Sphyrapicus thyroideus. This species is of interest in that the differences between the male and female (at all ages) closely parallel the differences between adults and juveniles in the related *S. varius*.

(12) *Neither adults nor juveniles have red or yellow on head; juveniles resemble respective adults (allowing for very minor differences).*

Hemicircus canente. It seems probable that *Nesocoleus* comes into this category but I can find neither juveniles of this species nor descriptions of them.

The aberrantly coloured *Asyndesmus lewis* does not fit readily into any of the above categories. Its juveniles are similar to but generally duller than the adults. They lack the silver collar and upper breast, have only traces of red on the face and have white sub-terminal spots (not present in the adult) on the feathers of the hind neck.

DISCUSSION. Thus, taking the woodpeckers as a whole, juveniles tend to be less, although often only a little less, conspicuously coloured than the adults. Sexual dimorphism is usually present in the juvenile plumage but is often much less marked than in the adult plumage. In species in which the adult males or adults of both sexes have the head almost entirely red the juveniles (where known) have appreciably less red on the head. Juveniles, taking all species into consideration, approximate more closely to the familial mean in the amount of red on their heads than do adults. This is well exemplified, within a small genus, by *Mulleripicus pulverulentus* and *M. fulvus* (see Text-fig. 4) and certainly suggests that the juvenile colour pattern resembles a previous stage in the species' evolutionary history, as Voous (1947) claimed for the red crowns of those species of *Dendrocopos* which show this feature only in their juvenile plumage. Certainly speciation in woodpeckers has involved both reductions and increases in the red areas of the adult plumages.

It is likely, however, that many features of the juvenile plumages may be functional and hence of selective value. This seems obvious in *Melanerpes erythrocephalus* and *Sphyrapicus varius*, whose much less conspicuous juvenile plumage must give some protection against aerial predators; both these species are partly migratory and often inhabit relatively open, although wooded, country. Under such conditions it may be of great advantage to the inexperienced juveniles to be less conspicuous. The

same is probably true for some other species in which the differences between young and adults are much less marked. In *Picus viridis*, for example, the more or less speckled and barred (but otherwise similarly coloured) juveniles are even less conspicuous when feeding on the ground than are the adults.

In the many species in which the juveniles are like the adults it is evident that here any advantages of a less conspicuous juvenile plumage are outweighed by others. Probably adult coloration is advantageous in the acquisition of territory or use of feeding areas in competition with adults. On the other hand the tendency in so many species, some of them congeneric with those showing strong sexual dimorphism, for the male and female juveniles to be almost alike, differing only in the female showing less extensive red or yellow areas than those of the male, may perhaps give other advantages which are more important for these species. It might, perhaps, lessen any tendency that might otherwise exist for either parent to "favour" young of one sex or it might better enable the female juvenile to hold her own in competitive strife with her brothers. Young *Dendrocopos major*, for example, may fight even in the nest hole (Sielmann, 1959). Where they are numerous, one sees much aggression and frequent fights between fledged young before (as well as after) they have moulted their juvenile plumage.

Where the juvenile lacks red on the head or has it more restricted than the adult it is tempting to suggest that this might function to reduce or inhibit aggressiveness on the adult's part, particularly in those species in which the juvenile lacks the red precisely on those parts, forehead and forecrown, which are presented to the adult when soliciting or taking food from it. This may be so but against this hypothesis is the fact that in some other species, including a large number of *Dendrocopos*, it is precisely these areas (forehead and forecrown) which are red in juveniles and not in the adult. It is often implied that the juveniles of those species of *Dendrocopos* that have a red nuchal patch have the entire top of the head red but in fact the young male, although having a red forehead and forecrown, is black on the nape where the adult male is red. The same is of course, true of the young female who has less red on her head (as a rule) than the young male. In these species of *Dendrocopos* the "replacement" of the red on the napes of adults by red on foreheads and crowns of juveniles reaches an almost bizarre state in the Red-cockaded Woodpecker *D. borealis* in which the adult male has a tiny red mark (the "cockade") on the sides on the hindcrown and the juvenile male an equally small red mark in the middle of his forecrown. It is, of course, feasible that in some species some inhibition of adult aggression could best be achieved by the young not presenting red markings to the feeding parent and in other species, in which the relative balance of fear and aggression differed, in their doing precisely that!

As *Dendrocopos major* is often instanced as a supposed example of a species in which the young are more brightly coloured than the adult it seems pertinent to digress here to say it is, in my opinion, very doubtful if the red foreheads of the juveniles make them more conspicuous to predators than are their parents. The same is probably true for the other species showing this character. All the boldly-marked black and white woodpeckers are, at least to human eyes, relatively conspicuous as compared with olivaceous or "ladder backed" species.

Section 2: Taxonomic notes on genera and species

MELANERPES, CENTURUS, TRIPSURUS AND LEUCONERPES

Peters (1948) included all the above genera in *Melanerpes* with the exception of *Leuconerpes*, which he retained as a monotypic genus for the White Woodpecker *candidus*. Hargitt (1890) had used a similarly broad conception of *Melanerpes* but had also included *candidus* therein. De Schauensee (1966) retains the genus *Leuconerpes* but notes that it "is perhaps not separable from *Melanerpes*." Selander & Giller (1963) give cogent reasons for treating *Tripsurus* as a synonym of *Centurus* but say that they do not feel justified in including both these genera in *Melanerpes*. However, I think that that is the most reasonable decision, unless all three genera are to be maintained. Both in its morphological characters and what is recorded of its ecology (see esp. Selander & Giller) *Tripsurus* seems perfectly to bridge the gap (such as it is) between *Centurus* and *Melanerpes* (sensu strictu). I provisionally maintain the genus *Melanerpes* as used by Peters, except as hereunder discussed.

The species *candidus* does not seem to me to be sufficiently distinct to warrant upholding the monotypic genus *Leuconerpes*. Its very distinct coloration, with entirely white head, parallels that of the few white-headed African barbets of the genus *Lybius*, the differences between most *Lybius* species and the white-headed forms being comparable to those between *candidus* and related species. Wetmore (1926) gave information on field habits of *candidus*, including its gregariousness (a feature also found in some *Melanerpes* species) and added that the genus *Leuconerpes* "in external characters . . . seems to be only slightly differentiated from *Tripsurus*." Scharnke (1931) concluded from studies of its tongue musculature that *candidus* was a primitive form and closely linked with *Sphyrapicus*. He found, however, several similarities between its tongue and that of *Melanerpes aurifrons*. Pending further and more detailed studies it is, I think, best to include *candidus* in the genus *Melanerpes*.

Melanerpes striatus

The Hispaniolan Woodpecker is a very distinct species which stands out among other species of *Melanerpes* by reason of its red rump, greenish yellow and black barred upperparts, yellow-green belly and, on closer investigation, its rather long tail and the marked sexual dimorphism in length of bill. For these and other reasons Selander & Giller (1963) argued that the monotypic genus *Chryserpes* should be used for this species. Later, however, after a detailed study of the species in the field in Hispaniola, the senior author (Selander, 1966) changed his opinion and was in favour of including it in *Centurus* (*Melanerpes*).

I do not know this species in life but on its museum characters I am entirely in favour of Selander's second decision. The barred pattern of its upperparts only differs essentially from other barred *Melanerpes* (*Centurus*) species in the greenish yellow instead of white on the paler parts of the feathers; this would seem to involve only the spread of lipochrome pigments to these areas. In this connection it may

be significant that *M. superciliaris* from Cuba has the white parts of the mantle suffused with yellow and *M. radiolatus* from Jamaica has much dark yellow on the lower breast and belly. The head colour pattern of *striatus* is rather like that of *superciliaris*. Its largely yellowish green coloration gives *striatus* a certain resemblance to some species of *Chrysoptilus* but it shows no trace of the conspicuously barred and spotted underparts of these. The red patch on the rump is shared by no other New World woodpecker except *Veniliornis kirkii* but I do not think any of the *Chrysoptilus* species or *V. kirkii* are very close relatives of *striatus*.

M. flavifrons, *M. formicivorus* & *M. chrysauchen*

The Yellow-fronted Woodpecker *M. flavifrons* and the Golden-naped Woodpecker *M. chrysauchen* are allopatric and seem best given specific rank although they certainly comprise a superspecies. The differences of the colour patterns of the heads of these two are very similar to those between the North and Central American forms of the Acorn Woodpecker *M. formicivorus* and the South American form (*flavigula*) of that species. The differences between nominate *chrysauchen* from Costa Rica and the Pacific slope of western Panama and the race *pulcher* from northern Colombia may be in part or whole due to character displacement in reference to the different races of *formicivorus* with which they are sympatric (see Text-fig. 5).

Melanerpes rubrifrons

Peters (1948) gives the Red-crowned Woodpecker *rubrifrons* specific rank but others (Stresemann, 1924, Greenway & Griscom, 1941, Todd, 1946 & Haverschmidt, 1956) have concluded that is a colour phase (morph) of *M. cruentatus*. I fully agree with this latter opinion which is substantiated by the specimens in the B.M. collection. Besides phenotypically "pure" specimens of each form there are several that are intermediate, to varying degrees.

The African Woodpeckers

All the sub-Saharan African woodpeckers seem to be more closely allied to one another than to any non-African species or genus. They are, I think, representatives of the stock ancestral also to *Picus* and *Dendrocopos*. Adaptive radiation has, however, resulted in similar but less marked divergences to those shown by woodpeckers in Eurasia and America. The second possibility: that the African forms are polyphyletic, with *Thripis* and *Dendropicos* closer to *Dendrocopos*, and *Mesopicos* and *Campethera* to *Picus*, is, I think, rather less likely. In spite of some remarkable general resemblances in coloration I think that the South and Central American green woodpeckers are more closely related to other New World forms, in the genera *Colaptes* and *Melanerpes*, than they are to African forms. When comparing, for example, species of *Dendropicos* and *Veniliornis* that look much alike, one finds that some details of their colour patterns differ from each other and are, respectively, closer to those of other African and South American species.

There have been divergencies of opinion as to how many genera of African wood-

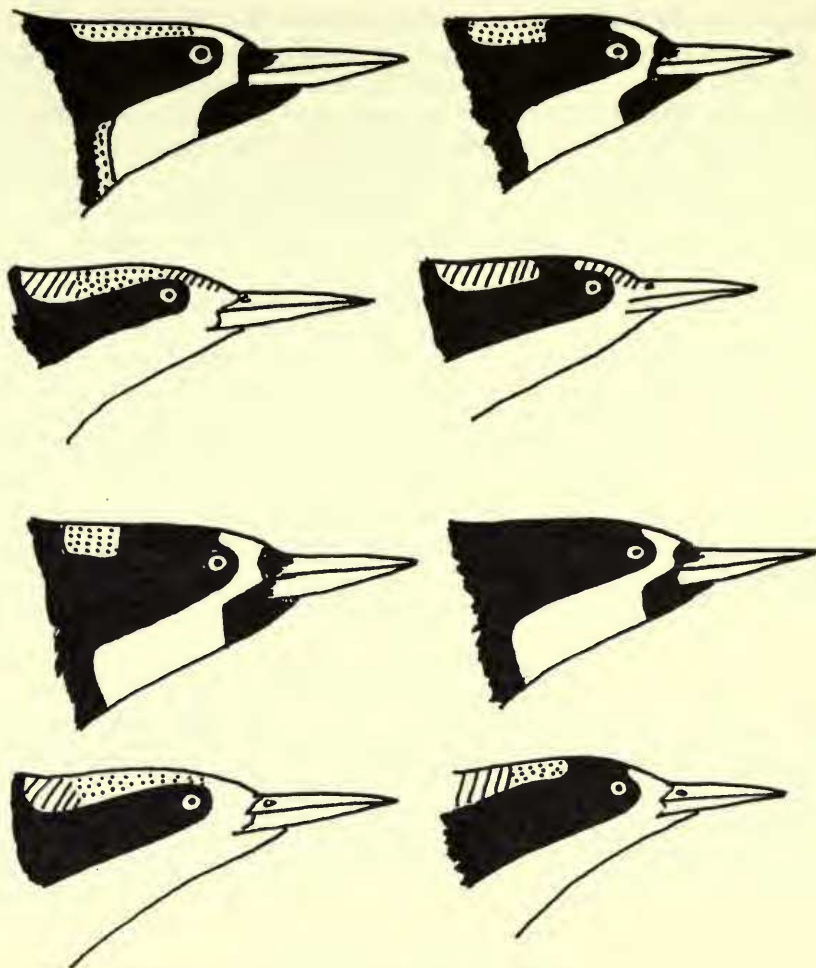


FIG. 5. Sketches to show colour patterns of heads of males (left) and females (right) of *Melanerpes formicivorus* (top) which overlaps in range with *M. chrysauchen* (second row) in Central America and of the form of *M. formicivorus* (third row) which overlaps with *M. chrysauchen* in northern South America. (See text).

peckers to recognize. Hargitt (1890) recognized the genera *Campethera*, *Dendropicos*, *Mesopicos*, *Thripas* and *Geocolaptes*, mainly on structural characters with emphasis on shape and size of bill. Other authors, notably Chapin (1939) recognized further genera but Mackworth-Praed & Grant (1957) followed Hargitt except for resurrecting the genus *Ipophilus* for the two species *obsoletus* and *stierlingi*. Peters (1948) put *elliottii* and *johnstoni* (now reckoned as a race of *elliottii*) in the genus *Polipicos* (following Chapin) but otherwise recognized the same genera as Hargitt and Praed and Grant although not with precisely the same allocation of species within them. I have followed Peters' nomenclature except where otherwise stated.

DENDROPICOS

Peters includes in this genus *fuscescens*, *stierlingi*, *elachus*, *abyssinicus*, *poecilolaemus*, *gabonensis* and *lugubris*. I concur with him in thinking that these species are probably more closely allied to each other than any is to species in another genus. This assumes, as I think is likely, that some differences of general coloration such as a tendency towards light, barred or spotted plumage in dry savannahs; darker, greener coloration in forests and the acquisition of a red rump have arisen independently in different (but related) stocks.

Their head markings suggest the *Dendropicos* species are nearer to *Thripias* and *Mesopicos* than to *Campethera*. The extreme similarity between *Dendropicos lugubris* and *Campethera nivosa* is, I think, due to parallel development but it may indicate true affinity in spite of differences in bill shape.

“ *Dendrocopos* ” *obsoletus*

Most writers on African woodpeckers (Bates, 1937, Chapin, 1939, Hargitt, 1890, Peters, 1948, Voous, 1947) put the Brown-backed Woodpecker, *obseletus*, in the genus *Dendrocopos* (or in *Yungipicus* which is now usually regarded as a synonym of *Dendrocopos*) but Grote (1928) and Bannerman (1933) placed it in *Dendropicos*. Voous in his monograph on *Dendrocopos* says that Grote and Bannerman had “abusively referred (it) to *Dendropicos*” and adds that this latter genus is quite distinct in having reddish or yellowish shafts to rectrices or remiges and usually in addition a distinct greenish tinge of the plumage. He considered, however, that *stierlingi* was correctly referred to *Dendropicos*. Mackworth-Præd & Grant, 1957, place *obsoletus* and *stierlingi* together in the genus *Ipophilus*.

I think that Bannerman and Grote were right to include *obsoletus* in *Dendropicos*. Among them the *Dendropicos* species show varying amounts of green coloration and/or yellow or reddish quill shafts. In two of them, *stierlingi* and *elachus*, this is reduced to a not very pronounced yellow tinge in the shafts of the wing and tail quills (*stierlingi*) or tail quills only (*elachus*). If either of these two species are compared with any other *Dendropicos* species it will be seen that the “gulf” between them, so far as yellow pigmentation is concerned, is greater than that between either one of them and *obsoletus*.

Voous links *obsoletus* with the pygmy woodpeckers of south Asia, *Dendrocopos nanus* and its allies, but in plumage pattern *obsoletus* is closer to *Dendropicos* species than it is to any of the Asian forms. In its coloration it is nearest to *elachus* although it lacks the latter's scarlet rump which is, in all probability, a species recognition mark serving to isolate *obsoletus* and *elachus* in the areas where their ranges overlap. Such species as *obsoletus* and *elachus* undoubtedly indicate the close relationship between “green” and “pied” woodpeckers or the potentiality for “green” and “pied” forms to evolve, in different geographical regions, from a common stock. I think, however, there is little doubt but that the true affinities of *obsoletus* are, as Bannerman and Grote decided, with *Dendropicos*.

Campethera bennettii, *C. scriptoricauda* & *C. nubica*

Benson (1952) gives evidence for the conspecificity of Bennett's Woodpecker *C. bennettii* and the Tanganyika Woodpecker *C. scriptoricauda*. In *C. bennettii vincenti* (Grant & Mackworth-Praed 1953) the throat colour of females is intermediate between the chocolate brown of *bennettii* and the creamy white of *scriptoricauda*, although it does not have the black spots of the latter. Some males of *vincenti* also have the ear coverts a less pure white than those of other forms of *bennettii*. Also a female *scriptoricauda*, from Blantyre, shows some approach to *bennettii* in colour, having fewer and smaller spots than usual, on a beige-tinted throat. It is unlikely that these specimens merely indicate occasional hybridization between two "good" species as there seem to have been no "pure" specimens of either *bennettii* or *scriptoricauda* collected within the range of *vincenti* and, more importantly, Mr Benson informs me (pers. comm.) that the calls and ecology of *bennettii* and *scriptoricauda* do not differ. I therefore agree with him that, on present evidence, *scriptoricauda* is best considered as a race of *bennettii*.

The very distinctive chocolate and white markings on the face and throat of the females in most forms of *bennettii* and, possibly, also the very white cheeks and intense red malar stripes of the male, probably function as isolating mechanisms in reference to *C. abingoni*, with which the chocolate-throated forms of *bennettii* overlap widely in range whereas *scriptoricauda* (and *C. nubica*) overlap only marginally with *abingoni*.

The Nubian Woodpecker *C. nubica* does not seem to differ in any significant plumage character from *C. bennettii scriptoricauda*; they differ only in the unspotted throat of *nubica*. Localities of specimens in the British Museum collections do not suggest any actual overlap of distribution. I provisionally maintain them as separate species, however, because Mr. C. W. Benson informs me that their calls differ, or at any rate those calls most usually uttered, and they differ in ecology.

Campethera nubica & *P. punctuligera*

I provisionally treat the Nubian and the Fine-spotted Woodpeckers, *nubica* and *punctuligera*, as members of a superspecies but I think it likely that they may prove to be conspecific. Although their respective ranges come close together in the southern Sudan and the eastern Congo I can find no evidence of both having been taken or identified in the same area (see also Chapin, 1939).

The form of *punctuligera*, *C. p. balia*, from the south-eastern Sudan and eastern Congo is largely intermediate in colour and colour pattern. The differences between the two forms are, chiefly, the size and formation of the spots on the breast and the presence (in *punctuligera*) or absence (in *nubica*) of spotting on the throat. One female of *balia* from Baginzi, Bahr el Gazal (B.M. No. 1919.10.7.23.) comes closer to *nubica* than most, having no spots on the throat, very dull underparts (less yellow tinge than usual in *punctuligera*) with the breast spots closely approaching those of *nubica* in pattern and general appearance although still much smaller than those of *nubica*. A juvenile from Angba, on the river Welle, also much resembles *nubica* in its breast spots.

Chapin (1939) says that the calls and habits of *punctuligera* and *nubica* are extremely similar and that "adherents of the Formenkreise theory" would surely consider them as forms of one species. A main difficulty and the one that chiefly prompts me still to treat them as species is that in appearance *punctuligera* could equally well be a form of *bennettii*, with which it is also allopatric. In fact there is an even closer resemblance in colour pattern between *punctuligera* and *bennettii scriptoricauda* than between the former and *nubica*. Present evidence suggests differences between the calls of *bennettii* and those of *scriptoricauda* but this negative evidence is of no great significance until the vocalizations of all three forms have been recorded in more detail. I suspect they may prove all to be members of a superspecies or even conspecific.

Campethera notata

I think Clancey (1958) is, right in suggesting that the Knysna Woodpecker *notata* and the Golden-tailed Woodpecker *abingoni* are possibly conspecific and certainly members of a superspecies. In spite of their great similarities, however, the pattern of the breast spots in *notata* is closer to those of *nubica*, *bennettii* and *punctuligera*, with none of which is *notata* sympatric, than to *abingoni* although such breast spots as those of *notata* could easily drive from the streaks of *abingoni* or *vice versa*.

Campethera cailliautii, *C. taeniolaema* & *C. maculosa*

These three species are all very closely allied, the Little Spotted Woodpecker, *cailliautii* and the Fine-banded Woodpecker *taeniolaema* being mainly allopatric. Their ranges overlap in the eastern Congo and adjacent areas where they appear, however, to be ecologically isolated, *taeniolaema* inhabiting the highlands and *cailliautii* the lowlands. They are very similar in coloration but *cailliautii* has the throat and face buffish with blackish, speckly-looking, barring whereas *taeniolaema* has the face and throat greenish white very finely barred with greyish olive.

From the Golden-backed Woodpecker *maculosa*, with which it is sympatric, *cailliautii* differs in the male having a slightly brighter red crown, greener and less gold-tinged upperparts and less boldly spotted on the throat. The females differ rather more markedly in *maculosa* lacking the red nape of *cailliautii*; she also has her entirely blackish crown spotted with deep buff, the spots on the head of *cailliautii* being pale buffish to white.

Campethera tullbergi

The rather distinct Tullberg's Woodpecker appears to be closest to *cailliautii* (*permista*) with which it is sympatric. The carmine patch on the carpal area of the wing probably serves as a species-specific recognition mark in reference to *cailliautii*. I fully concur with Peters (1948) that *C. wellsi* should be considered a race of *tullbergi*.

Campethera nivosa

The Efulen race of the Buff-spotted Woodpecker, *efulensis* Chubb, appears to be inseparable from nominate *nivosa*. One of three specimens from the type locality

(*Efulen, Cameroon*) can be matched by a specimen of *nivosa* from Portuguese Guinea. The large series from Kumba, Cameroons, vary from typical "*nivosa*" to typical "*efulensis*" in colour. The races *poensis* and *herberti* are slightly differentiated but recognizable.

MESOPICOS

The Grey Woodpecker *M. goertae* and the Olive Woodpecker *M. griseocephalus* are very closely related and could certainly be considered as members of a superspecies or even as conspecific but for the fact that their ranges overlap in parts of Kenya and north-eastern Tanzania. We have, however, no records of both species from precisely the same place although there are specimens of both from north-eastern Tanzania, *goertae* from Nabara and *griseocephalus* from Same. In and near the area of apparent overlap they appear to be ecologically separated, *griseocephalus* being confined to highland forest.

The only absolute colour differences between the adults are the darker grey head and golden-olive breast of *griseocephalus*. In *goertae* juveniles of both sexes have red on the head, the male usually rather more than the female. Some works on African birds imply that in *griseocephalus* the young are, except for being duller, like the respective adults. There are only six juvenile *griseocephalus* in the British Museum collection, some unsexed, others sexed as males. All of them have red on the head; in some of them the red is less extensive than in others and I suspect these may be females. Juveniles of *griseocephalus* are, incidently, paler and greyer in colour than adults and thus come even closer to *goertae* in appearance than do the adults.

A few remarks on geographical variation in both species: From West Africa (Senegal, Gambia, etc.) across to Uganda and the southern Sudan *M. goertae* shows no striking differentiation, if allowance is made for individual differences (from the same area some birds may have an orange-red belly patch and others not) and those due to wear (which are often considerable). Within this region there is a tendency for birds from the more northern arid areas to be palest and to have more distinct barring on the wings and upperparts, those from the southern areas to be darker and duller. Specimens from Gambia to Uganda tend to have little or no orange-red, only yellowish, on the belly. Those from the extreme north-east of this area (parts of Southern Sudan) are *more* like those of Senegal in coloration than are the latter to Gambian birds!

I think it best to recognize three races within the above areas: nominate *goertae* from Senegal, the paler *königi* (Neumann, 1903) from the Lake Chad regions, parts of French Niger and French Sudan and *centralis* (Reichenow 1900) and agree with Mackworth-Praed & Grant (1957) in thinking *agmen* (Bates, 1932) and *oreites* (Grote, 1923) best treated as synonyms of *centralis*. This is an admittedly wide but I think workable interpretation of *centralis* but it must be borne in mind that no hard and fast line can be drawn between any of the above-mentioned forms of *goertae*. To the east of its range *centralis* intergrades with *abessinicus* (Reichenow, 1900).

M. griseocephalus persimilis (Neumann, 1933), described from the Highlands of

Angola (Benguella) was recognized by Peters but has since been commonly treated as a synonym of *ruwenzori* (Sharpe, 1902). In the original description *persimilis* was separated on its smaller size. Besides the rather slight size difference our specimens from Angola, southern Congo and Tanzania mostly show quite conspicuous paler barring on the flanks which is absent from specimens of *ruwenzori* from Ruwenzori and Lake Kivu. I have, therefore, recognized *persimilis*.

Mesopicos elliotii

Chapin (1939) & Peters (1948) both use the genus *Polipicus* Cassin for Elliot's Woodpecker which was previously (Hargitt, 1890) and subsequently (Mackworth-Praed & Grant, 1957) included in *Mesopicos*. In structure of bill *elliotii* (with which *johnstoni*, formerly given specific rank, is now reckoned conspecific) is nearer to *Mesopicos* than to other African genera but in its other external characters it seems to be as close to *Campethera*. The two genera are, however, closely allied. It seems preferable to leave *elliotii*, at least provisionally, in *Mesopicos* rather than to place it in a monotypic genus.

Mesopicos elliotii sordidatus (Bates, 1928) was described from a juvenile from Oku, west of Kumbo, Cameroons. Its supposed racial characters are merely those of the juvenile plumage. There are now two adults from Oku in the British Museum collection, these do not differ from examples of *M. e. johnstoni* of which I therefore consider *M. e. sordidatus* a synonym.

THRIPIAS

Peters (1948) includes the Bearded Woodpecker *namaquus*, the Fire-bellied Woodpecker *pyrrhogaster* and the Golden-crowned Woodpecker *xanthocephalus* in the genus *Thripias*. Many other authors, e.g. Hargitt (1890), Chapin (1939) and Grant & Mackworth-Praed (1957) have put *pyrrhogaster* and *xanthocephalus* in *Mesopicos*, presumably mainly on account of their proportionately shorter wings (than those of *namaquus*) and maintained *Thripias* as a monotypic genus.

I think Peter's arrangement is best. These three species all agree in having a relatively long and straight bill, black nuchal region in both sexes and similar characteristic facial markings. Against these I do not think that the proportionately longer bill and tail of *namaquus* warrants its generic separation. *T. namaquus* seems to link the other two *Thripias* species (as reckoned here) with *Campethera* rather than with *Mesopicos*. In this connection it may be mentioned that the female of *Campethera bennettii* has facial markings rather similar to, although not identical with, those of the *Thripias* species.

Geocolaptes olivaceus

I think the Ground Woodpecker is most closely related to other African forms and that its resemblance to some of the American flickers, *Colaptes*, (near which it is usually placed in systematic lists,) is due to convergent adaptations for terrestrial or semi-terrestrial life. It differs from the *Colaptes* species but very closely resembles

Mesopicos goertae and *M. griseocephalus* in colour pattern except for the barred tail and the vestigial red malar stripes of the male. Both these are, however, very widespread characters in "green" woodpeckers and occur, *inter alia*, in some *Campethera* species.

It seems likely that *olivaceus* evolved from some form ancestral both to itself and to *goertae* and *griseocephalus*. It may well have retained (or developed) red malar stripes as a species-specific recognition mark in reference to *griseocephalus* (or its ancestor). The present apparently obsolescent state of the malar markings might indicate that the development of greater divergence in size and ecology has now obviated the need for such distinguishing markings between these two forms.

Notes on *Picus*

Peters (1948) includes in *Picus* the former genera *Chrysophlegma*—species *mentalis* and *flavinucha*, and the monotypic *Callolophus*—species *mineaceus*. Hargitt (1890) included the latter in *Chrysophlegma* also although he placed the smaller yellow-crested forms, *puniceus*, *chlorolophus* and *chlorigaster* with the "typical" green woodpeckers in the genus *Gecinus*. Within Peter's broad and inclusive conception of *Picus* the species fall into three rather distinct groups which are not precisely the same as those suggested by former allocations of species between *Gecinus* (or *Picus*) and *Chrysophlegma*. The latter genus was defined as having "wing rounded . . . nasal ridge almost obsolete, culmen ridge very blunt, tail two thirds length of wing" and later by Stuart Baker as having ". . . bill more curved and nasal ridge almost obsolete, well-developed nuchal crest." These definitions have, apparently, restrained those who recognized *Chrysophlegma* from including in it the species *chlorolophus*, *chlorigaster* and *puniceus*, which have rather straighter culmens than the other yellow-crested species.

The group of most typical *Picus* species comprises *viridis*, *canus*, *vallantii*, *awokera*, *viridanus*, *vittatus*, *squamatus*, *xanthopygaeus*, *erythropygasus* and *rabieri*. All these are relatively long-billed forms with fairly straight culman, nuchal crest absent or slight, primaries marked whitish and black or grey, and except in one race of *canus*, no red or chestnut colour on wings. *P. rabieri* has a more rounded wing and rather shorter bill than the others and approaches the next group in these features.

The species in the second group are characterized by having yellow nuchal crests, shorter bills and, one species excepted, red coloration or at least a reddish tinge, on the wings. They comprise *flavinucha* and *mentalis*, which in addition to the characters listed above also have black and chestnut primaries and a spotted patch on the throat, and *puniceus*, *chlorolophus* and *chlorigaster* which have rather straighter culmens, no chestnut on their primaries which are dark and whitish, varying amounts of red on the head, and are smaller in size. To some degree these three forms link the original "*Chrysophlegma*" species to the first group but they are, I think, much more closely allied to the former.

The third group consists of the single species *mineaceus*. This has a long and broad occipital crest, relatively short, broad bill, barred plumage pattern both above and below and rather harsh, coarse-feeling plumage. Although it may be justifiable

to include *mineaceus* in the present enlarged conception of *Picus*, (and certainly this is more reasonable than allying it with *flavinucha* and *mentalis* and yet not putting *puniceus*, *chlorolophus* and *chlorigaster* in the same genus), it is a very distinct species. It appears to be a link between *Picus*, via *Picus puniceus*, and the Rufous Woodpecker *Micropternus* to which it shows some approach in proportions, coloration, plumage pattern and plumage texture.

I think it possible that more comprehensive studies might indicate that the species in this second group are less closely allied to those in the first group than are the latter to such Ethiopian genera as *Campethera* and *Mesopicos*.

Picus canus

In the eastern part of its range, where it and *viridis* do not overlap, the Grey-headed Woodpecker *canus* much more nearly approaches the Green Woodpecker *viridis* in size and proportionate length of bill. The only similarly-sized green woodpeckers which it overlaps in eastern Asia are *P. erythropygius* and *P. rabieri*, which are very distinct from *canus*, with striking colour differences. *Picus dedemi* of Sumatra seems rightly put as a form of *canus* in spite of its different colouring, with bronzy carmine, with a hint of green, replacing the green and olive of *canus*. The racial variation within the Palearctic populations of *canus* has been very fully discussed by Vaurie (1959).

Picus vaillantii

Vaurie (1965) put North African Green Woodpecker *vaillantii*, as a race of *viridis* and earlier (1959) anticipated this decision on the grounds that in everything except the black malar stripe of the male, which he considered an "alternate character" to the red and black malar stripe of the male *viridis*, *P. viridis sharpei* of the Iberian peninsula "bridges the gap" between *viridis* and *vaillantii*. He pointed out *vaillantii* had already been listed as conspecific with *viridis* by Goutenoire (1955) and that Dr. David Snow, who has observed this species in the wild, was also in favour of this decision.

I cannot, however, see that *sharpei* is intermediate between [other races of] *viridis* and *vaillantii* except in bill shape and I do not think that minor details of size, size of bill or tone of general colour, in all of which *vaillantii* comes nearer to *viridis* than it does to European forms of *canus*, are of much significance when dealing with a geographically isolated "green woodpecker". Especially in view of the amount of geographic variation shown by both *viridis* and *canus* and the obvious close relationship of the above three forms and the Japanese Green Woodpecker *P. awokera*. The female of *P. viridis sharpei* has the feathers of the forehead and crown red (or, to be more precise, these areas all tipped with red) as in other races of *viridis*, whereas these areas are without any red in females of *vaillantii*. Incidentally, the red tips on the nape feathers of *vaillantii*, appear longer than and somewhat different in texture from those of *viridis* or *canus*.

While *vaillantii* may be more closely allied to *viridis* than it is to *canus* or *awokera*, the differences in colour patterns of their heads, lack of red on malar stripe of male *vaillantii* and black and grey instead of red forehead and crown of female, might be

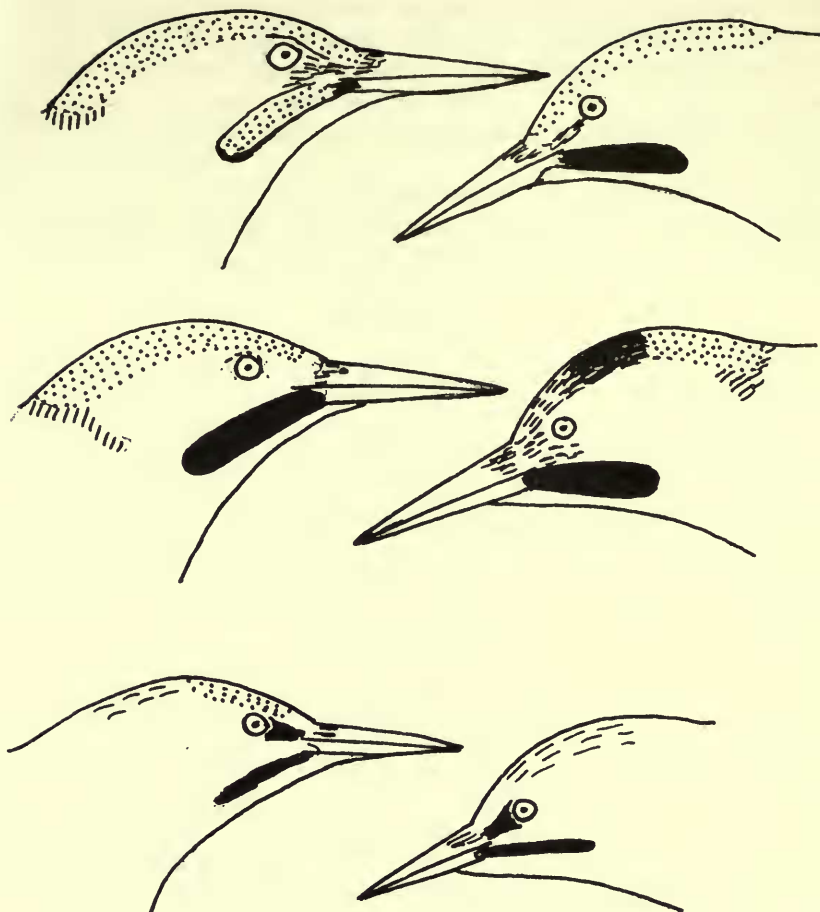


FIG. 6. Diagrammatic sketches to show colour patterns of heads of males (left) and females (right) of *Picus viridis* (top, *Picus vaillantii* (middle) and *P. canus* (bottom).

pre-adapted to act as isolating mechanisms should the two ever overlap in range. Of its more striking plumage characters *vaillantii* shares one (crown and nape of male red) with *viridis*, two (no red on malar stripe of male, forehead and crown of female grey or grey and black) with *canus* and two (red on nape only of female, forehead and crown of female grey or black and grey) with the more geographically distinct *awokera*. I think it best, therefore, to give *vaillantii* specific status although it can, at least provisionally, be put in the same superspecies as *viridis*.

Picus rabieri

This is a very distinct species but, in spite of its rounded wings and somewhat different colour pattern, I think it is an offshoot of the *viridis* group although in wing shape and in its rather short bill it shows some approach (convergence) towards the *flavinucha* group.

Picus squamatus*, *P. viridanus*, *P. vittatus* & *P. xanthopygaeus

These species form a closely related group and are essentially alike in coloration and colour pattern. The Red-rumped Woodpecker *P. erythropygius* is related to this group, as its colour pattern especially in the eye-striped morph, clearly indicates.

The Scaly-bellied Green Woodpecker *P. squamatus* overlaps in part of its range with the Little Scaly-bellied Woodpecker *P. xanthopygaeus* from which it differs in being much larger, having very conspicuous black and white malar stripes, the upper breast plain greyish green without squamate markings and conspicuously barred central (and other) tail feathers.

P. xanthopygaeus overlaps with the Burmese Scaly-bellied Woodpecker *P. viridanus* and marginally with the Laced Green Woodpecker *P. vittatus* from both of which it differs in having inconspicuous (almost obsolescent) malar stripes, more streaked (longitudinal squamate markings) throat and yellow or greenish yellow instead of yellowish green rump and upper tail coverts.

P. vittatus and *P. viridanus* are extremely similar, differing in appearance only in *viridanus* having the streaky-looking squamate markings of the underparts extending forward onto the upper breast and throat where they are, however, less clearly defined than lower down. As given in many standard works the ranges of the two would appear to overlap in parts of Eastern Burma and south-western Siam. In the fairly extensive series of both in the British Museum (Natural History) there are no specimens of both species from any one area with the exception of one specimen of *viridanus*, allegedly from Tenasserim, where only *vittatus* normally occurs. I think this probably represents some error in labelling.

Robinson & Kloss (1923) say that "where the ranges of the two species touch or approach there is not the slightest sign of intergradation". In view of the extremely slight differences between them I do not find this statement very convincing. There are two specimens in the British Museum, No. 1887.8.10.1556 from Mergui and No. 1887.11.1.95 from "Burmah", which are absolutely intermediate between "typical" *vittatus* and *viridanus* at first appearance. On closer examination they are seen to have squamate markings on the upper breast although these are fainter than usual in *viridanus*. It is significant, perhaps, that in all specimens of *viridanus* these squamate markings are least developed on the upper breast and throat, contrary to what one might expect if they functioned as a species recognition mark in reference to *vittatus*.

Deignan (1963) puts *viridanus* as a race of *vittatus* and, although he does not there give his reasons for so-doing, all the evidence I have been able to find suggests that he is quite right in this decision.

Picus chlorolophus* & *P. chlorigaster

The number of races of the Small Yellow-naped Woodpecker *chlorolophus* that has been described tends to obscure the main difference which is between the populations in peninsular India and Ceylon and those from elsewhere. The former, at one time given specific status as *P. chlorigaster*, are not only geographically isolated but in some characters come closer to the related Crimson-winged Woodpecker *P. puniceus*

resembling it and differing from typical *chlorolophus* in having blackish lores, instead of whitish as in *chlorolophus*, and the top of the head entirely red. In the amount of red on their wings they are intermediate.

The three forms, *chlorigaster*, *chlorolophus* and *puniceus* are allopatric except that an isolated race of *chlorolophus* (*rodgeri*) occurs in the mountains of Perak. There is thus a very limited geographical overlap of this form with *puniceus* although there is apparently no ecological or altitudinal overlap (Robinson, 1928). This montane race is rather dark in colour and thus superficially somewhat intermediate between *chlorolophus* and *chlorigaster* but in its main features it agrees with the former, with which its affinities clearly lie. I think it is preferable to treat *chlorigaster* as a member of a superspecies, together with *chlorolophus* and *puniceus*, rather than as a race of *chlorolophus*.

DENDROCOPOS

Voous (1947) shows that the American and Asiatic "ladder-backed" woodpeckers in this genus all inhabit areas that were not covered with Pleistocene land-ice and which, in North America, represent the glacial forest refuges. He considers all these ladder-backed species to be (relatively) closely related in spite of their present discontinuous ranges.



FIG. 7. Diagrammatic sketches to show colour patterns of heads of a typical Old World *Dendrocoptes* (*major*), a typical New World ditto (*villosus*) and *Picoïdes trydactylus* (left to right) (In all species the heads shown are of females).

All American ladder-backs agree with other American *Dendrocoptes* species, and differ from most Old World *Dendrocoptes* species, ladder-backed and otherwise, in lacking red on the ventral regions or under tail coverts. They also have a similar head pattern, with a dark post-ocular band, to other American *Dendrocoptes* species. I think these facts indicate that all the New World *Dendrocoptes* species are more closely related to each other phylogenetically than any one of them is to any Old World form.

It seems more likely that the "ladder-back" pattern (so common in woodpeckers generally) has developed, or been retained if it was a primitive feature, independently in both Old and New Worlds, as an adaption to relatively open or well-lighted habitats in which it probably has protective value, than that some factor in the American environment has caused two or more phylogenetically distinct *Dendrocoptes* stocks to lose all trace of red on the underparts and to acquire similar facial markings subsequent to their arrival in America. In this connection it is pertinent that in some species of *Melanerpes* the adults are plain backed and the juveniles ladder-backed

and in the Three-toed Woodpecker *Picoïdes tridactylus* some races are ladder-backed and others not (see Text-fig. 8).

Of Old World species the "dwarf" woodpeckers, *D. minor*, *D. kizuki*, *D. nanus et al.*, come nearest to the American forms in their colour patterns and are, I think, closest to them phylogenetically.

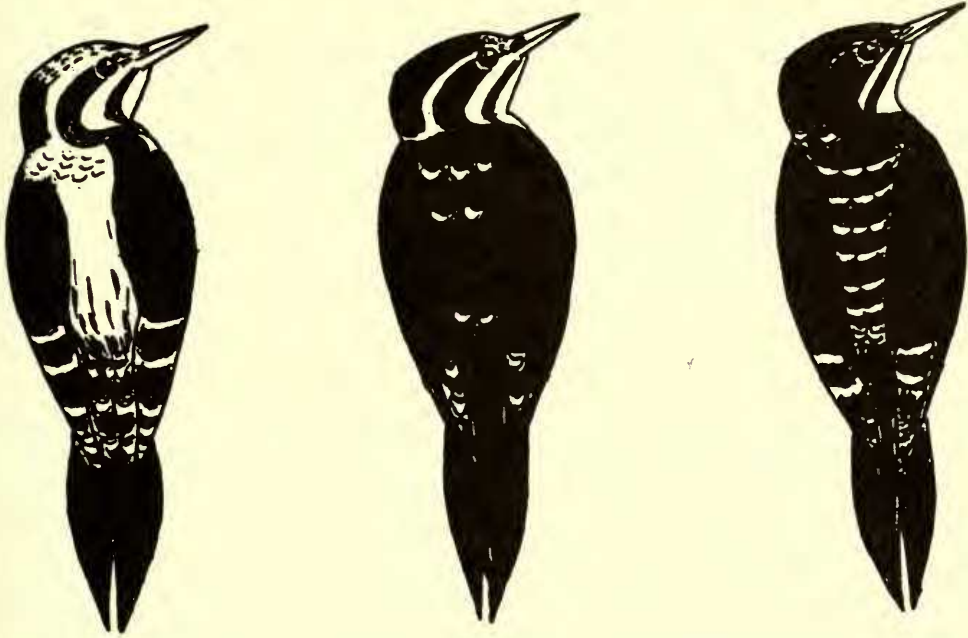


FIG. 8. Diagrammatic sketches to show variation in back pattern within a species: Females of *Picoïdes trydactylus* from Sweden (left), South-eastern Tibet (middle) and eastern North America (right).

The Hairy Woodpecker *D. villosus* and the Downy Woodpecker *D. pubescens* are now very largely sympatric. They presumably derived from a common ancestor at a relatively recent date as their colour patterns are virtually identical. They also show similar geographical variation although this, by itself, is of course, no argument for close relationship.

Nuttall's Woodpecker *D. nuttallii* and the Cactus Woodpecker *D. scalaris* are also close relatives. They appear not to be sympatric and descriptions of their calls do not suggest any great difference of voice. They may prove to be conspecific but provisionally are, perhaps, best treated as members of a superspecies. The Red-cockaded Woodpecker *D. borealis* is, I think, closely allied to them. Its strikingly different facial pattern seems to have been achieved by the extreme reduction of the usual (in American *Dendrocopos*) black post-ocular stripe so that only a vestige of this marking remains. I think, however, that the great similarity in position and extent of the red on the head in this species and the Old World *D. kizuki* is due to convergence, within related stocks, and does not indicate that *borealis* is closer to

kizuki than are other American species. The juveniles of *borealis* and *kizuki* do not, apparently, resemble one another in position of red on the head as *kizuki* is said to resemble the adult in this respect. The Arizona Woodpecker *D. arizonae* and Strickland's Woodpecker *D. stricklandi* are allopatric, they are close to one another in appearance, voice, behaviour and ecology (Davis, 1965). On its upperparts *stricklandi* has a colour pattern intermediate between that of completely ladder-backed species and those, such as *arizonae*, with uniform dark back and rump. Individuals of *arizonae* which show traces of a barred dorsal pattern do, however, occur (Davis, 1965). The two are otherwise similar in colour but differ in *stricklandi* having dark streaks on the underparts with some indication of barring on the flanks, whereas *arizonae* is spotted, but the differences are less impressive when the markings on the individual feathers are compared. I think *arizonae* and *stricklandi* are best considered members of a superspecies.

The two South American forms the Striped Woodpecker *D. lignarius* and the Chequered Woodpecker *D. mixtus* differ from all North American *Dendrocopos* species in having their central tail feathers strongly barred with white and they are generally lighter and more "spotty" in appearance. They show much resemblance in plumage pattern to *Veniliornis spilogaster* and I think this may indicate close relationship between *Veniliornis* and *Dendrocopos*. They agree, however, with the northern forms in general overall colour pattern. From their visual characters one would certainly suspect them of being conspecific but they apparently overlap in range, both being found in Nequen and the eastern Rio Negro in Argentina (Peters, 1948, Olog, 1963). Two specimens in the British Museum from Cordova, Argentina, (B.M. Nos. 1889.2.26.112 and 113) appear to be intermediate between *D. lignarius* and *D. mixtus berlepschi*. The male of the two agrees with *mixtus* in the extent of the red on its head but both are closer to *lignarius* in plumage pattern, which is, however, extremely similar in the two species (?) in any case. These two have longer bills than our specimens of *berlepschi* but we have only two of the latter and, at least in *lignarius*, this feature seems prone to individual variation.

The White-headed Woodpecker *Dendrocopos albolarvatus* is rather aberrant in colour pattern and its tongue is said (Voous, 1947) to be less extensible than in other (all other?) *Dendrocopos* species. Its external features, particularly the typically dendrocopine correlation of a red nape in the adult adult male with a red crown and black nape in the juvenile indicate that Peters was right to include it in *Dendrocopos*.

Dendrocopos darjellensis

Measurements of our specimens seem to indicate a less clear-cut difference between nominate specimens of the Darjeeling Pied Woodpecker, *darjellensis*, and *D. darjellensis desmursi* (J. Verreaux) than did those measured by Vaurie (1959). We have, however, no topotypical specimens of *desmursi* from Sikang and only a few from Yunnan. Our only specimen of *fumidus*, from the Naga Hills, does not show the characters claimed for this race (Ripley, 1951) and thus tends to confirm Vaurie's opinion that *fumidus* should be considered a synonym of *darjellensis*.

This species overlaps widely with the Crimson-breasted Pied Woodpecker

D. cathpharius. The two are nearly identical in coloration but differ much in size. Their yellow-tinged cheeks and underparts, red breast bands and heavy streaking on the underparts are considered by Voous to be primitive characters. Whether this is so or not these characters might function now as species-specific signal markings.

Dendrocopos leucopterus

I concur with Voous (1947) and Vaurie (1959) in thinking that it is better to give *leucopterus*, provisionally, specific rank. This, however, is mainly on grounds of convenience. I think Vaurie has rather over-emphasised the differences between *leucopterus* and *major*. I have seen no juvenile specimens of *leucopterus* so do not know if I should think them so distinct from juvenile *major* as they are said to be. It seems, however, pertinent to remark that although, as Vaurie says, juvenile *major* of both sexes have red on the crown, that on the female is normally less extensive than the male's. So the fact of the juvenile female of *leucopterus* having (always?) an entirely black crown may not be of specific significance.

Dendrocopos doraë

Although at first glance the Arabian Woodpecker is rather like some of the species in the African genus *Dendropicops* it seems most closely allied to the Eurasian forms of *Dendrocopos* and is now rightly included in that genus.

I think that *doraë* may be closest to *medius*; to which it bears much resemblance when allowance is made for "fading" of the black areas to darkish brown (already often shown to some extent in some individuals of *medius*) and for reduction of the white areas. In size, texture and colour of the red crown feathers, and the streaking on its flanks it is very like *medius*. Indeed, the differences between these two woodpeckers are very similar in kind, although greater in degree, to those between the Arabian form of the Magpie *Pica pica* and its more northerly representatives. In *doraë*, like most *Dendrocopos* species but unlike *medius*, the female lacks red on the head but I do not think this feature of *medius*, which is unique within the genus, argues against their close relationship. *D. medius* and *D. leucotos* are unquestionably close relatives, but differ in this feature as they do in size and bill shape.

Dendrocopos analis, *D. atratus* & *D. macei*

I provisionally follow Peters & Deignan (1945) in treating *analis* as a form of the Fulvous-breasted Pied Woodpecker *macei*. They differ slightly in size, in *analis* having a spotted rather than a streaked breast, white ground colour on underparts and central tail feathers and upper tail coverts barred with white instead of uniformly black. They do not, however, differ in colour pattern of the head. Intermediates occur (*vide* Deignan, 1945) in the Chiang Mai area of Siam.

Voous (1947) suggests that *macei* and the Stripe-breasted Pied Woodpecker *atratus* may be conspecific, quoting Standford & Ticehurst (1939) that where they appear geographically to overlap in range in northern Burma *macei* is a lowland and

atratus a highland form. He mentions specimens of *macei* obtained by Hume in Manipur, Assam and implies that these showed some intergradation with *atratus*.

At least some of these Manipur specimens are in the British Museum collection and do not seem to differ from other specimens of *macei*, collected elsewhere. When they are compared with specimens of *atratus*, also collected in Manipur, the differences between them are at least as great as between specimens of both from elsewhere. That is, *macei* differs in being smaller, having an unstreaked lower throat, the underparts creamy rather than dusky yellowish and with not very prominent dark streaks, as against very prominent dark streaks in *atratus*. The red on the ventral region does not usually extend so far forwards, the red of the head is a little less bright and the red feathers are a little dissimilar in texture. These differences also hold for *analisis*, which has, in addition, tail and rump feathers barred with white. *D. analisis* and *D. atratus* overlap widely, geographically, but may be ecologically isolated. Thus some of the differences between *analisis* and *macei* might have originated as species-specific recognition marks in reference to *atratus*.

Dendrocopos major

Vaurie (1959a) puts the race *parroti* (Hartert) from Corsica as a synonym of the Sardinian form *harterti* (Arrigoni). I prefer to recognize *parroti* as there appears to be very little overlap in bill length and the bills of all our specimens of *parroti* are noticeably more massive than those of specimens of *harterti* of the same sex. In view of the only slightly differentiated and intergrading continental races of this woodpecker that are currently recognized it seems better not to lump these two island forms.

Vaurie considers it most probable that *D. m. tianshanicus* represents inter-specific hybridization between *major* and *leucopterus*. With one exception our specimens all seem nearer to *major* and I provisionally treat them as a form of *major* and not as hybrids. The exception to this, mentioned above, is a female from the Tekkes Plain (B.M. No. 1931.7.8.259) which was originally identified as *leucopterus* and later re-identified by Vaurie as *tianshanicus*, because it had a wing measurement of 137 mm. as against 120-129 mm. for 23 females of *leucopterus* measured by Vaurie and because he considered the white spots on its wings too small for *leucopterus*. I think this bird was correctly identified originally. The very large measurement of its right wing appears to be due to the make-up of the skin. The left wing measures only 130 mm. and 11 other females of *leucopterus*, picked at random, have wing measurements ranging from 125 to 131 mm. The white spots on its wings do not appear to be significantly smaller than those of some other specimens.

PICOIDES

I agree with Delacour that this genus is very close to *Dendrocopos*. Its lack of red pigments, or rather their replacement by yellow; its flatter bill and its lack of a fourth toe are, in combination, perhaps just sufficient grounds for keeping it in a separate genus. It is certainly convenient to do so and the two *Picoïdes* species are, unquestionably, much more closely related than either is to any other.

However, although *Picoïdes* seems to have diverged a little further from the *Dendrocopos* species in the course of evolution than these have from one another it is, I think, likely that it may be phylogenetically closer to the American *Dendrocopos* species than these are to Old World forms.

The colour pattern of *Picoïdes tridactylus* is very close to that of *Dendrocopos villosus*. This is especially so with the northern Old World forms of *tridactylus*. The relatively greater amount of difference between the New World forms of *tridactylus* and *villosus* may be due to character displacement although in some other Holarctic species or superspecies there is a tendency for the New World representatives to show a greater amount of melanin pigment than the Old World forms (e.g. *Numenius phaeopus*, *Branta bernicla*). In this connection it is of interest that nominate *P. t. tridactylus* has a broad white stripe down its back like *D. villosus* whereas the American forms, e.g. *P. t. fasciatus*, show white cross-barring very like that of the "ladder-backed" *Dendrocopos* species and similar in position and extent to that of *D. stricklandi*.

The Arctic Three-toed Woodpecker *P. arcticus*, which is entirely American in distribution, has a wholly black back with, sometimes, a hint of barring indicated by white tips to one or two feathers. In the large amount of black in its plumage generally *arcticus* stands in about the same relation to American forms of *tridactylus* as these latter do to most of the Old World forms of their species. Although now largely sympatric with the smaller *tridactylus*, *arcticus* must, presumably, have evolved in isolation from *tridactylus* or proto-*tridactylus*. The very dark, and now apparently geographically isolated, Tibetan form of *tridactylus*, *P. t. funebris*, is suggestive in this connection as it shows similar, and nearly as great, contrast to the northern Old World forms of its species as does *arcticus* to American forms of *tridactylus*.

Sapheopipo noguchii

The Okinawa Woodpecker, originally included in the genus *Picus* (Seebohm, 1887), was placed by Hargitt (1890) in the monotypic genus *Sapheopipo*, which he having: "wing very long and pointed; tail only equal to the second primary and falling short of the longest by about an inch". It is found only in Okinawa, in the central Ryukyu Islands, south of Japan.

The general coloration of *noguchii* is dark olive, more or less suffused with red, especially on the tips of the feathers, on back, rump and underparts; with dark brownish-black wings and tail. It is thus, superficially, most like the dark red Sumatran form of *Picus canus*, *P. c. dedemi*. It has, however, very clear indications (see Text-fig. 9) of head and breast markings nearly identical to those of many *Dendrocopos* species and quite unlike those of any species of *Picus* or *Dinopium*. Also those parts of the primaries that are not visible, or at any rate would not be conspicuous, when the wings are closed have white markings similar to and I think homologous with those of *D. leucotos owstoni*, the very dark race of *D. leucotos* from the northern Ryukyu islands. The legs and irides of *noguchii* and *owstoni* agree in colour although their bills do not (Kuroda, 1925).

The difference of coloration between *leucotos* and *noguchii* is very similar to what one finds between many other species and their island derivatives, for example the pigeons *Columba arquatrix* and *C. pollenii*. They seem to have involved, assuming *noguchii* to be derived from *Dendrocopos* stock, simply a spread of dark pigment together with some lessening of its intensity and the spread into some of these dark areas of red or yellow pigments; or, perhaps, their revelation through their no longer being completely masked by melanin pigments. The pale colour of the bill might be similarly caused. In proportion and in the shape and structure of its bill *noguchii* is quite close to *leucotos* although its bill is proportionately longer, a common feature with island forms. Its type of sexual dimorphism is identical with that of *leucotos* and several other *Dendrocopos* species. *D. leucotos owstoni* is, presumably, a more recent invader of the Ryukyu Islands that is already beginning to evolve in the same direction as has *noguchii*.

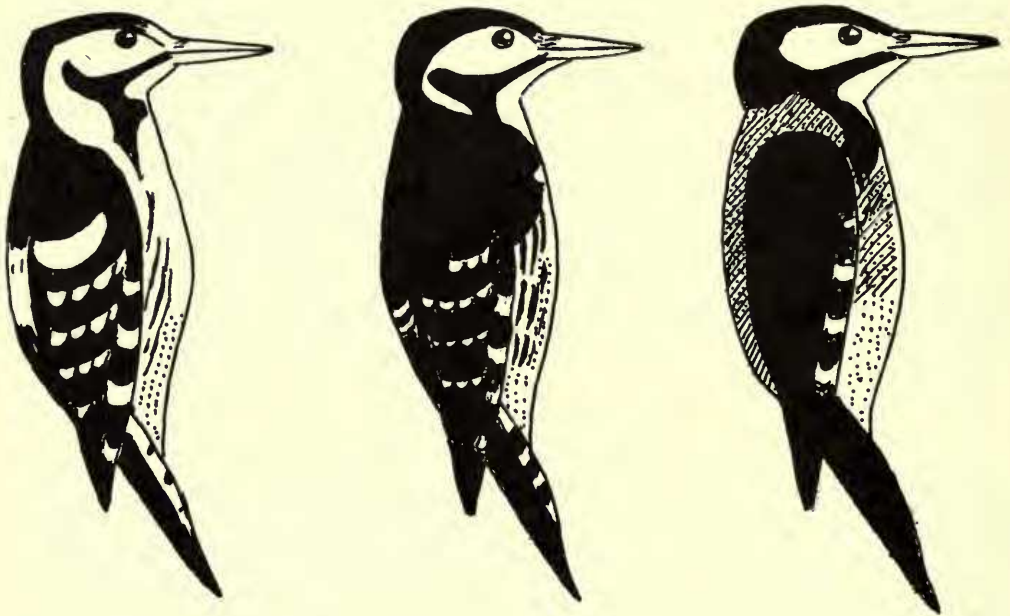


FIG. 9. Diagrammatic sketches to show resemblances and differences of colour patterns of *Dendrocopos leucotos* from northern Europe (left), same species from northern Ryu-kyu Islands (middle) and *Sapsheopipo noguchii* (right).

I think that *noguchii* is an offshoot of *Dendrocopos* stock and is rather more likely to have derived from *Dendrocopos leucotos* subsequent to the speciation of the latter than from a more primitive common ancestor to them both. It is said (Kuroda, 1925) to be found on or near the ground in damp woods or bamboo jungle and never in tall trees during the day (he does not say whether it roosts in tall trees but this is, perhaps, implied). This suggests that *noguchii*'s ecology may have already diverged considerably from that of typical *Dendrocopos* species and this, together with its unusual coloration, may, perhaps, justify retention of the monotypic genus *Sapsheopipo*.

If, however, further studies should show that it does not differ so markedly in habits as Kuroda's notes suggest and that there are no striking anatomical differences I would be in favour of treating *Sapheopipo* as a synonym of *Dendrocopos*.

CHRYSOCOLAPTES & DINOPIUM

Delacour (1951) suggested that the absence of the fourth toe is not of great phylogenetic significance in woodpeckers and that in this character *Brachypternus* with its greatly reduced fourth toe, placed by Peters (1948) in the synonymy of *Dinopium*, forms a link between the three-toed *Dinopium* species and *Chrysocolaptes* with four well-developed toes. I agree with his opinion on both points; there can be no doubt that the species comprising the above genera are all closely allied. I provisionally maintain the genus *Chrysocolaptes* mainly on grounds of taxonomic convenience. This can, perhaps, be further justified by the fact that the three species involved—*lucidus*, *festivus* and *validus* seem very close to each other. All, apart from having four toes, agree in having some white on hind neck and mantle, admittedly vestigial in *lucidus*, almost identical facial markings which are, however, approaching obsolescence in *validus*, and bills that are longer and more massive than those of *Dinopium*. Except in the case of *Dinopium javanense* and *Chrysocolaptes lucidus*, wherever two species of either (or both) of these two genera overlap widely in range they show fairly striking differences of colour pattern.

The very similarly-coloured Golden-backed Three-toed Woodpecker, *D. javanense* and the Golden-backed Woodpecker *C. lucidus* are extensively sympatric and, in general, show similar geographic variation. They are most alike in western India, Burma and much of Malaysia where, except for the not very striking difference in the pattern on face and throat, colour differences between them are slight or non-existent. *C. lucidus* is, however, a larger bird with proportionately much larger bill. In other areas where they overlap the two show greater differences in coloration. On Java *lucidus* (race *strictus*) has a female with the top of the head yellow and rather obscurely spotted, and both sexes have only a tinge of red on the rump, whereas the *javanense* female has a black and white streaked crown and both sexes have a conspicuous red rump.

On Palawan *lucidus* has a very distinct race (*erythrocephalus*) in which both sexes have a red face and pink throat, with the usual dark striations rather reduced, the female has the top parts of her head a mixture of red and yellow-olive with light dull yellow spots, the individual feathers being red near the base, then olive with a yellow terminal spot. The Palawan form of *D. javanense* (*everetti*) is very distinct, having a boldy striped buffish and black face and the female a black forehead and crown and red nape. It is noteworthy, however, that, compared with other forms of *javanense*, this race shows parallel development to *lucidus* on Palawan, in having more red on the head than is usual in the species: females of other forms of *javanense* have no red on the nape and the males no red on the malar region as has *everetti*. They also agree in having the dark and light facial markings less pronounced than in most other forms of their respective species.

Chrysoclaptes lucidus

I provisionally follow Peters (1948) in his wide conception of this species because, on external characters, it is not possible to make any logical division among the many races or presumed races of *lucidus*. It is, however, quite possible that some of the island forms, especially in the Philippines, may have already reached specific level.

Like previous workers, I cannot separate specimens from South India from those from southern Malaya although the latter are, on average, a slightly lighter golden-yellow on the upperparts. There seems no alternative, therefore, but to continue to employ the name *chersonesus* for both these populations although it is likely that, in a phylogenetic sense, *chersonesus* from southern India are more closely allied to *guttacristatus* from Bengal than they are to *chersonesus* from the Malay Peninsula.

On the different Philippine islands the races (?) of *lucidus* show great variation of head colour (besides other differences). These are comparable to the differences of head colour between undoubted species of the *Chrysocolaptes-Dinopium* group elsewhere. This is no doubt due at least partly to the lack of any closely related sympatric species on most of these islands. Nominate *lucidus* from Mindanao is, perhaps rather unfortunately, a rather nondescript or intermediate form and as it has indistinct facial markings, mixed red and yellow upperparts and the top of the female's head yellowish and spotted it is difficult to ally it with any one, or even any one of the main groups of Philippine forms rather than another. The interesting sequence of the immature plumages of *guttacristatus* (and other races of *lucidus*?) is described in the section on juvenile plumages.

Dinopium shorii & *D. javanense*

The Himalayan Golden-backed Three-toed Woodpecker and *D. javanense* are very closely allied and must have derived relatively recently from a common ancestor but they appear now to overlap without interbreeding in northern Burma. There are specimens of both from Thayetmayo and the Arrakan Hills, in the British Museum. They appear to keep or even slightly to accentuate their minimal plumage differences—pale bases to the red head feathers in *shorii*, slightly different pattern of streaks on the throat—where they overlap. Admittedly hybrids between the two would be difficult to recognize. There is a slight difference of size and bill length between them and, no doubt, this correlates with differences of ecology.

Dinopium rafflesii

I concur with Peters in thinking it preferable to put the monotypic genus *Gauropicoides* (species *rafflesii*) into the synonymy of *Dinopium*. The Olive-backed Three-toed Woodpecker, *rafflesii*, seems to link *Dinopium* with *Gecinulus*, agreeing with the former in most characters but with *Gecinulus* to some extent in its softer feather texture and generally dark and rather concolorous body plumage. The wing markings are similar in both genera.

The genus *GECINULUS*

I maintain this genus for the Pale-headed Woodpecker *grantia* and the Green Bamboo Woodpecker *viridis*. These two closely allied forms differ from the green woodpeckers of the genus *Picus* in having proportionately small bills and only three toes; also in some plumage characters in which they are closer to *Dinopium*. Although rather discrete they appear, as has been mentioned above, to be linked with *Dinopium* by *rafflesii* and probably represent a link between *Picus* and the *Dinopium-Chrysocolaptes* group.

DRYOCOPUS & PHLOEOCEASTES

Peters (1948) placed the American species *pileatus*, *lineatus*, *erythroops* and *galeatus* in the genus *Dryocopus* together with the old world forms *martius* and *javensis*. Presumably he did this because their outer hind toes are not longer than their outer front toes (Peters, 1948, introduction, p. 6). The characters of a narrower nasal shelf and nostrils nearer the culmen, which he says are correlated with the shorter outer hind toe, do not appear to be valid as there is much variation between species; on these characters *lineatus*, at least, seems to fit better with those species which have a longer outer hind toe. I do not think this relative length of the outer hind toe is,

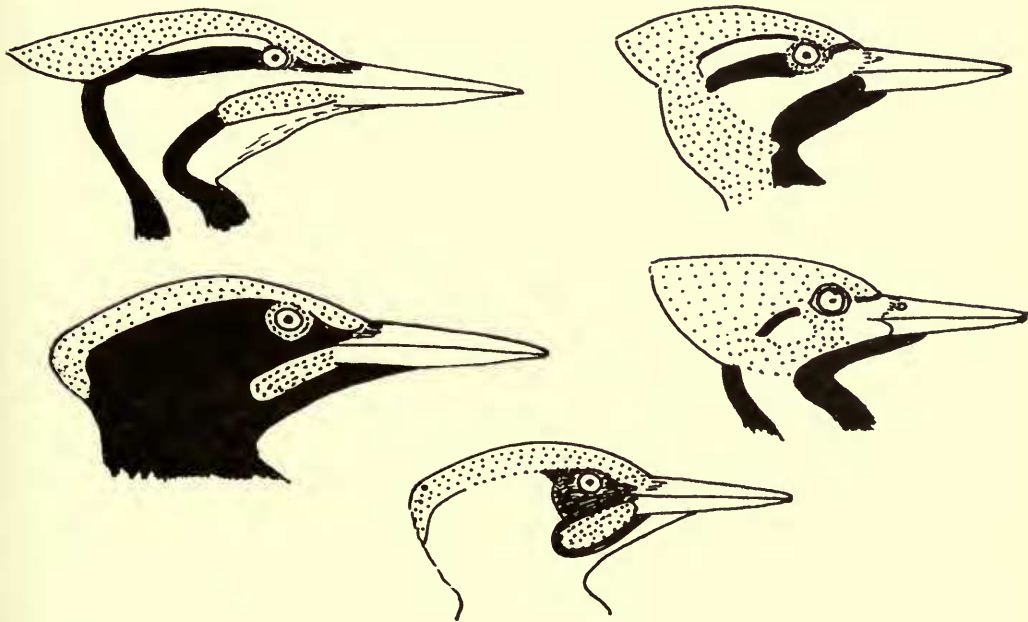


FIG. 10. Diagrammatic sketches to show colour patterns of heads of *Phloeoceastes lineatus* (top left), *Dryocopus javensis* (bottom left), *Picus viridis* (bottom middle), *Phloeoceastes haematogaster* (top right) and *P. melanoleucos* (bottom right).

by itself, a very important character. Their distribution and their plumage characters, especially the colour patterns of their heads all suggest that the American species placed by Peters in *Dryocopus* are closer to the species included by him in the genus *Phloeocastes* than they are to Old World forms. I therefore think it best to place them in *Phloeocastes* and restrict *Dryocopus* to the two Old World species *martius* and *javensis*.

I think it possible that *Dryocopus*, as above restricted, might prove to be more closely related to other Old World genera, such as *Mulleripicus* and *Picus*. Kilham (1959) was impressed by the great similarity between some of the behaviour patterns he had observed in *pileatus* and some described for *martius* (Blume, 1956) but comparisons of these two with both (other) *Phloeocastes* species and *Mulleripicus* are needed. Most of sketches and descriptions in Blume's comparative study of European woodpeckers (Blume, 1961) suggest to me that the displays, and possibly even the calls, of *martius* bear a more close resemblance to those of *Picus viridis* than to those described for *pileatus* by Kilham.

Phloeocastes divides readily into the *lineatus* species-group comprising *lineatus* (syn. *erythrops*), *pileatus*, *schulzi* and *galeatus*, all of which have rather softer, denser plumage with consequently longer nuchal crests and tend to have proportionately smaller bills, and the *melanoleucos* species-group, comprising *melanoleucos*, *guatemalensis*, *pollens*, *haematogaster*, *rubricollis*, *robustus* and *leucopogon*.

Within the *lineatus* group *pileatus*, *lineatus* and *schulzi* are closer to each other in colour patterns than any of them is to *galeatus*. This may give a false impression, as the very differently coloured (largely buffish brown) head and underwing of *galeatus* may be the result of selection for species-specific markings in reference to *lineatus* which it overlaps widely in range. *P. pileatus* does not overlap any congener and *schulzi* would appear to have only a marginal overlap with *galeatus* and *lineatus* at the northern edge of its range. Both *pileatus* and *schulzi* have concolorous black underparts unlike any other close relatives. This might, however, be due to some environmental factor as these two are in predominantly temperate climates north and south, respectively, of the ranges of other *Phloeocastes* species.

The species in the *melanoleucos* group all appear to be very closely related to each other. Within this group it is possible that relatively greater differences in colour pattern between any two species may not indicate comparable phylogenetic disparity as such differences may have evolved as isolating mechanisms in reference to each other. Although all species show differences in colour pattern these are, on the whole, most marked, and often correlated with differences of body proportions, in species that overlap widely in range. It is notable that both this and the *lineatus* group have evolved some forms predominantly white and others predominantly buff or chestnut on the under wing.

I follow Peters in thinking it best to give specific rank to both *guatemalensis* and *melanoleucos*, although they can certainly be considered as members of a superspecies. Further studies may, however, show that they are in fact conspecific and if so the rather striking differences in colour patterns of their heads may be a case of character displacement as *melanoleucos* overlaps in range with *robustus* whose male has an almost entirely red head like that of *guatemalensis*.

Phloeocastes lineatus & *P. erythrops*

Peters (1948) says that it has been suggested that *erythrops* is a subspecies of the Lineated Woodpecker *lineatus* but that, if specimens have been correctly identified, they overlap over a wide area. He treats *erythrops* as a good species but remarks that "The inter-relationships of the *lineatus-erythrops-schulzi* group are quite involved and require additional field study".

Van Rossem (1934) and De Schauensee (1966) have both presented evidence that *erythrops* and *lineatus* are conspecific. I have compared specimens of both from Sapucay, Paraguay and they differ in no character except the presence (in *lineatus*) or absence (in *erythrops*) of white on the scapular region. Van Rossem states that some specimens of *erythrops* show white markings on the shoulder region and one of our specimens has one white-edged feather in this region. I think the evidence suggests that *lineatus* is dimorphic over the southern-most part of its range and that *erythrops* is merely a black-shouldered morph of this species.

CAMPEPHILUS & IPOCRANTOR

Hargitt (1890) followed Cabanis & Heine (1863) in placing the Magellan Woodpecker in the monotypic genus *Ipocrantor*; Peters (1948) placed it with the ivory-billed woodpeckers in the genus *Campephilus*. Peters was, presumably, led to this because its rather large size (in comparison with *Phloeocastes* species), soft, glossy black plumage, large white wing patches and the long crest of the female combine to give it a very similar general appearance to an ivory-bill. Although it is possible that *magellanicus* does represent a divergence from the same stock as produced the ivory-bills, subsequent to the latter's splitting off from ancestral *Phloeocastes*, I think this rather unlikely.

The coloration and colour-patterns of the heads of both *magellanicus* and the ivory-bills are closer to those of *Phloeocastes* than they are to each other. In both *magellanicus* and the ivory-bills the colour pattern of the head seems to represent a modification and some degree (considerable in *magellanicus*) of simplification of a pattern typical of *Phloeocastes*. This simplification has involved a reduction in the amount of red in the male ivory-bills and its increase in the male of *magellanicus*. The white wing patch of *magellanicus* might represent a restricted version of that found in the ivory-bills but could equally (in both) be a development from the white or light bars that some *Phloeocastes* species show on (some of) the inner webs of the primaries and secondaries. The under wing pattern of *magellanicus* is closer to that of *Phloeocastes melanoleucos* and *P. guatemalensis* than it is to that of *Campephilus*. The bill of *magellanicus* is dark, not white or cream-coloured. Some species of *Phloeocastes* have pale bills (others have dark bills).

It is, I think, likely that the features in which *magellanicus* agrees more closely with the ivory-bills than it does with *Phloeocastes* species: length of crest of female, relatively lax, glossy plumage and rather long tail (all, probably, correlated characters) are due to convergence in related stocks but that each is, phylogenetically, at least as closely related to *Phloeocastes* as to the other. I think, therefore, that it is preferable to retain the monotypic genus *Ipocrantor* for *magellanicus*. The only

reasonable alternative, and one that seems to have much to recommend it, would be to place all these large, related, predominantly black, white and red woodpeckers in the single genus *Campephilus*. I feel, however, that it would be premature for me to do so now in view of the work currently being done in the U.S.A. on the habits and ecologies of the American woodpeckers which will, doubtless, soon provide other and perhaps firmer grounds for taking or refraining from this course.

Variant individuals

The commonest plumage variation in woodpeckers, occurring in individuals of many green-backed and golden-backed species, is for the green or golden parts of the plumage, especially on the mantle, to be more or less suffused or mottled, with red. This correlates with the existence of several red-backed forms closely related to or even conspecific with green-backed and golden-backed forms. Other variants in the British Museum (Nat. Hist.) collection are listed and described below.

Picus vittatus

A male from Pulau Langkawi, Malay Peninsula (B.M. No. 1936.4.12.586) shows an apparent reduction of red and yellow pigments. Its breast, underparts and sides of face are paler and more buffy than in normal specimens. The green of its upperparts is a colder hue, less tinged with yellow, and the red parts of its head a light flame-orange instead of the deep scarlet-crimson of normal birds.

Dendrocopos assimilis

A male from Khipri, Sind (B.M. No. 1898.12.12.331) has the red on the head replaced by straw yellow except for the nuchal region and a line extending thence above each eye, where it is orange-red, not the normal dark scarlet.

Dendrocopos himalayensis

A supposed male from near Simla (B.M. No. 1887.8.10.7) has the belly, flanks and much of the lower breast red, instead of this colour being confined to the under tail coverts and post-cloacal area as in normal specimens. Surprisingly, if it is correctly sexed, it shows much less red on the head than normal, this being confined to the tips of only about a third of the crown feathers. It would seem strange if the bird exhibited an excess of red pigment in one area yet a decrease of it elsewhere and I am inclined to think that it may be a female, in which case (the female having normally no red on the head) its head coloration would, like that of its underparts, represent an increase of red.

Dendrocopos syriacus

An adult female (B.M. No. 1888.11.1.564) shows partial albinism. It has many white or partially white feathers on normally black areas of head, back and wings. The distribution of red is normal.

Dendrocopos atratus

A presumed female from the Southern Shan States of Burma (B.M. No. 1903.12.24.53) shows an interesting coloration as a result of partial loss of melanin pigment. It gives a general impression of having most of the normally black areas replaced with light grey. More closely examined it shows, on its upperparts, a narrow edging of more intensely pigmented (darkish grey) plumage posterior to every white marking (except where this comes to the end of the feather) and a similar but broader dark edge immediately anterior to it. This is most clearly seen on the secondaries but holds good for all other feathers. On the outer webs of the outer primaries the dark grey areas are more extensive. The tail shows ill-defined light and darker grey transverse barring but the modified, supporting, central feathers have their tips and the edges of both webs more heavily pigmented, a dark brownish grey. The top of the head is noticeably darker than most of the back, being, at least so far as the tips of most feathers are concerned, a very brownish grey, almost blackish. Due, presumably, to the reduction of melanin the underparts look much paler and more yellowish than normal, the dark streaks are greyish brown, not brownish black, and the red under tail coverts lighter and brighter.

It would be interesting to know whether the areas (tail tips, primary edges] etc.) which show stronger pigmentation in this individual also have in fact more melanin in normal birds where it is not visually evident. As they all seem to be areas that are likely to need "extra" strengthening, this would seem probable.

Dinopium benghalense

A male from southern Konkan (B.M. No. 1887.8.10.1957) and a male from Khandeish (B.M. No. 1880.1.1.225) both have many red-tipped feathers in the malar region, giving much the impression of the type of black-enclosed red malar stripe found in males of *Picus viridis*. Normally *D. benghalense* has no red in the malar region in any plumage phase.

A female from Sind (B.M. No. 1941.5.30.1391) shows reduction of red and yellow pigments. The normally golden parts of the mantle are a pale straw yellow, the normally scarlet nuchal crest more or less cream, intermixed with some partially orange-pink feathers.

A female from Lucknow (B.M. No. 1887.8.10.1932) although normal in coloration, seems worth mentioning here. It has an abnormally long bill with decurved culmen which looks more like a Hoopoe's bill than a woodpecker's. The culmen measures 64 mm., as against 36 to 38 in normal females, and overlaps the under mandible by 7 mm. The bill tips are narrow and flexible and it is impossible to believe that the bill could have been used at all for wood-pecking. The bird had evidently been able to obtain food as is adult and in good plumage.

Phloeocastes lineatus

Male from eastern Ecuador in post-juvinal moult (B.M. No. 1940.12.5.93). Has the central part of the crown and nuchal region bright straw yellow, tinged orange,

instead of red. The red on the forehead and sides of head is a little lighter in hue than usual.

Dinopium javanense

Three females of the race *intermedium* show some trace of red in the head plumage. No. 1921.12.31.92, from western Siam has several male-type red feathers, two of them long nuchal feathers, on the left side of its head. No. 1927.6.5.419, from Tonkin, has one red-tipped but otherwise female-type feather above its left eye and No. 1927.6.5.1587, from Cochinchina, has several red-tipped but otherwise sexually intermediate-looking feathers.

Many of the above variants involve partial loss of pigmentation and are comparable in appearance, and probably in origin, to relatively common varieties in other groups. It is, however, of interest that where this involves only the partial substitution of red by yellow, as in the *Dendrocopos assimilis* and the *Phloeocastes lineatus*, it is comparable to one of the more conspicuous differences in coloration often found between related species of woodpeckers. This, of course, is also true of the second type of variant included above, where individuals show red on areas not normally so-coloured in their sex or species.

SUMMARY

Some aspects of taxonomy and relationships of the woodpeckers are described and discussed. Certain close resemblances in coloration and ecology are due to convergence. In all geographic regions inhabited by woodpeckers the smallest species are about the same size; the same is true for the largest species except that there are no large arboreal species in the Ethiopian region. The typical forms of sexual dimorphism and the exceptions to them are described.

Juvenile woodpeckers usually have bright pigments similar to, but not always identical with, those of the adults. When all species are considered, the juveniles approximate more closely to the family average in the amount of red or yellow on the head than do the adults. In no instance, however, is the juvenile plumage considered to be more conspicuous than the adult male's.

Leuconerpes is treated as a synonym of *Melanerpes*. The species *obsoletus* is considered to be referable to *Dendropicops* not *Dendrocopos*. *Geocolaptes* is related to other African genera, not to *Colaptes*. It is thought that all the New World species of *Dendrocopos* are more closely related to each other than any one of them is to any Old World species. *Sapheopipo* is a recent derivative of *Dendrocopos*. Some of the Philippine Island races of *Chrysocolaptes lucidus* show colour differences comparable to those shown by different species of the *Chrysocolaptes-Dinopium* group elsewhere. The New World forms currently placed in *Dryocopus* seem better placed in *Phloeocastes*. Unless all the large black, white and red American woodpeckers are to be treated as congeneric, it is best to retain the monotypic genus *Ipocrantor* for the species *magellanicus*.

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